DEPTH PERCEPTION IN THE PIGEON

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To Richard

Thanks for everything

To my parents

CONTENTS

DECLARATION

This thesis describes original research carried out by the author during the tenure of an Australian Government Postgraduate Research Award in the Department of Behavioural Biology, Research School of Biological Sciences and the Department of Psychology, School of General Studies. The ophthalmoscopic experimental measurements in Chapter 5 were carried out jointly with Liz Reymond. The work described in this thesis has not previously been presented for a degree at this or any other university and to the best of my knowledge and belief contains no work previously written or published by another person unless due reference is made in the text. The animal experiments were carried out according to the guidelines set by the Committee on Animal Experimentation, Proposal Number R. BB. 20. 83.

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ABSTRACT

Stereopsis depends on both stimulation of corresponding retinal points of each eye and a neural site in which integration of the two monocular visual signals combine. Stereopsis has only been shown to be present in frontally eyed animals that have a predatory life style. This thesis presents the first evidence for the existence of a binocular depth mechanism in a granivorous bird (*Columba livia*) that does not hunt and catch prey and possesses a panoramic field of view by the lateral placement of the two eyes. The pigeon has a small region of binocular overlap which was found in this thesis to be symmetrical about the eye-beak axis.

The behavioural procedure used was a discrete trial simultaneous operant conditioning paradigm. Pigeons were found to be able to discriminate depth in 'Frisby' stimuli that were based on a clinical test of stereopsis used with young children (see Hinchliffe, 1978). The birds' performance on the depth task was superior under binocular rather than monocular viewing conditions. In addition, partial disconnection of the two half brains severely impaired binocular depth perception.

The smallest depth difference discriminable at threshold in terms of retinal disparity, was found to be 1 minute of arc. This depth acuity is better than the spatial frequency acuity of the pigeon and surpasses that predicted by the sampling mosaic of the retina. Thus the depth acuity is likely to reflect stereoacuity.

In all birds, there is almost complete decussation at the optic chiasm. Thus, binocular convergence must occur at a subsequent stage in the visual system. It was found that bilateral lesions of the Wulst, the telencephalic target of the thalamofugal system, had no

effects on the behavioural depth discriminations, even when tested at the psychophysical limits of binocular depth perception. In contrast, interruption of binocular neural integration by separation of the two half brains at the level of the tectal and posterior commissural systems resulted in behavioural deficits on the depth tasks.

Taken together, the results give support for the presence of stereopsis in a lateral eyed, non-predacious bird. Hence stereopsis is not an emergent capacity bestowed on a relatively small number of elite animals, but may be a fundamental attribute of vertebrate vision.

PLATE CAPTIONS

TABLE CAPTIONS

FIGURE CAPTIONS

COMMON ABBREVIATIONS

AP	anterio-posterior
CA	anterior commissure
CP	posterior commissure
criterion	three successive sessions in which performance exceeds 90% correct
CT	tectal commissure
Δ C	change in initial post-operative performance relative to criterion
d	viewing distance
DSO	supraoptic decussation
DSO_d	dorsal supraoptic decussation
DSO_v	ventral supraoptic decussation
D10	depth 10 stimulus
DV	dorso-ventral
EW	Edinger-Westphal nucleus
F1	first head fixation
F2	last head fixation
Frisby stimuli	depth stimuli based on a clinical test for stereopsis using real depth targets
HA	hyperstriatum accessorium
HD	hyperstriatum dorsal
HIS	hyperstriatum intercalatus suprema
IHA	nucleus intercalatus hyperstriati accessorii
IOT	interocular transfer
LACE task	task in which depth is present over the entire positive stimulus giving a 'lacy' two-dimensional appearance
LACE 6	LACE 6 stimulus
L1	transection of supraoptic decussation and anterior commissure
L2	transection of the anterior commissure

CHAPTER ONE

BACKGROUND LITERATURE REVIEW

AND GENERAL INTRODUCTION

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This thesis is an investigation into the pigeons' perception of the relative distance (depth) between objects in space. Location of objects in space with respect to oneself (egocentric) or other objects (exocentric) is a necessary and often highly refined function of many animals. In the bird, the location of objects is necessary for survival and is implicit in a range of activities from the accurate location of food with respect to the beak, to the estimation of the position of obstacles while flying and the detection of predators. One may argue that detection is not synonymous with the location of an object. With respect to a predator it may be enough to be aware of existence and direction alone. Yet, in detecting an object, an animal often has to contend with breaking camouflage (see plates 1.1 - 1.4). An effective way to do so is to locate the desired object or animal with respect to the background - that is - perceive the object stereoscopically. Such depth perception is clearly an advantage, not only for detection of predators, but also for the detection of food sources.

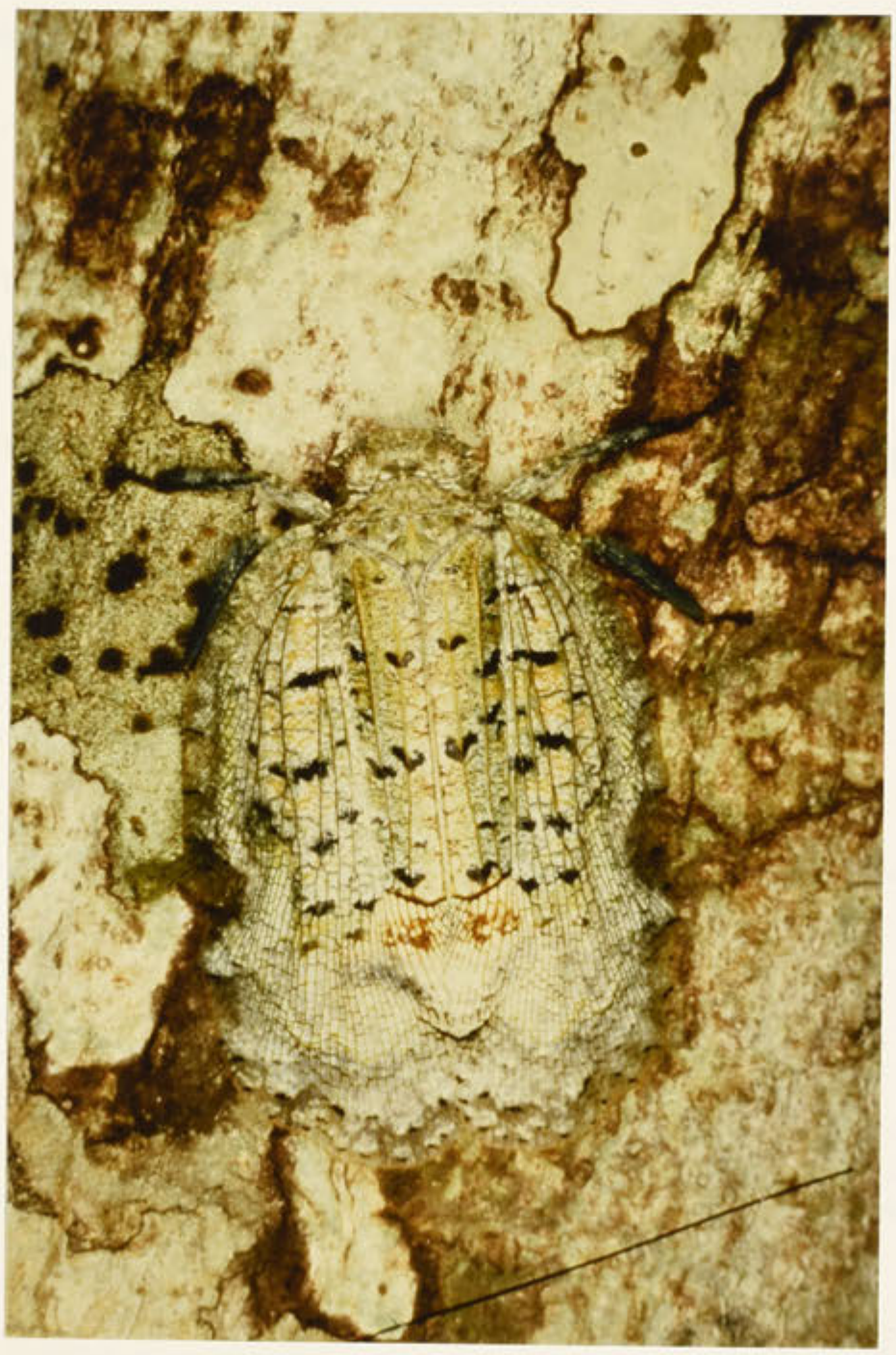
Indeed, one may again use the camouflage example to point out the universal effectiveness of the few principles of camouflage employed throughout the animal kingdom (Cott, 1966). Hence, although obvious differences exist between the optic arrays of various environments, the underlying spatial metric and optical principles are common to all species. Thus, in the literature review which follows, I have described the perception of depth in animals in terms of what is known about our own abilities to perceive the location of objects in space. Classically, the perception of depth, intimately related to egocentric absolute distance estimation, has been considered as the perceptual integration of a number of cues. These cues may be elicited on the basis of vision with a single eye, or may require the coordinated activity of the two eyes.

Plate 1.1 Camouflage I: Short horned grasshopper (*Acrididae*), Shark Bay, Western Australia (Photograph courtesy of D. Knowles).

Plate 1.2 Camouflage II: Huntsman Spider (*Sparrassidae*), Yuin Station, Western Australia (Photograph courtesy of D. Knowles).

Plate 1.3 Camouflage III: Map Butterfly Cyrestis niven (*Nymphalidae*), Kutai Reserve, Kalimanton (Photograph courtesy of D. Knowles).

Plate 1.4 Camouflage IV: Lantern Fly (*Fulgoridae*), Eunung Reserve, North Sumatra. Did you notice a similar species to the left of the butterfly in plate 1.3? (Photograph Courtesy of D. Knowles).



Many of the monocular cues for the perception of depth are considered 'higher order' and are referred to as secondary cues, while the binocular and oculomotor cues are considered as primary cues to three dimensional space. This distinction between primary (accommodation, convergence, motion parallax and stereopsis) and secondary cues (relative size, interposition, linear and aerial perspectives, and light and shade) is reflected in the earliest modern observations of depth perception, which were guided by the question of whether appreciation of space was learned or innate.

In the following review, some early studies on the nature/nurture issue are examined. Some examples of secondary monocular cues to depth are then presented, particularly as they relate to the birds' visual capabilities. However, most of the review is dedicated to the primary cues to depth, as these have received by far the most attention in recent years. In particular, emphasis is placed on binocular depth perception. As little work has been done in this field on birds, much of the discussion centres on the current state of knowledge of binocular depth perception in our own visual system and in other animals.

1.1 THE NATURE/NURTURE ISSUE

In 1873, Spalding commented on the behaviour of young dark-reared chicks on their first exposure to visual space:

> In from two to fifteen minutes they pecked at some speck or insect, showing not merely an instinctive perception of distance, but an original ability to judge, to measure distance, with something like infallible accuracy.

A number of investigators, notably Grinnell (1921), Benner (1938) and Pumphrey (1948) (see Shinkman's review, 1962), Bird (1926) and Hess (1950, 1956, 1961) have subsequently examined the question of the nature/nurture issue. They have used the response of young chicks pecking at grain as an indicator of depth discrimination.

Shepard and Breed (1913) concluded that practice effects in pecking were complete after two days and that any subsequent improvement was due to maturation. Bird (1926) divided the pecking response into three components and noted the proportion of misses, hitting but not seizing the grain and seizing but failing to swallow. He found that increased accuracy, mostly that seen in the missing error, was due to maturation. Reduction in the number of missing reactions also occurred in the absence of practice, although practice aided in reducing the error (Cruze, 1935).

These findings confound the effects of sensory and motor development, so it is not clear what role maturation plays in the discrimination of depth. The perception of depth is not a sufficient condition of the peck response. Furthermore, there was no attempt to break depth perception into the component cues.

1.2 SECONDARY MONOCULAR CUES TO DEPTH

1.2.1 Light and Shade

The use of light and shade as a cue to depth was examined by Benner (1938, cited in Walk, 1965). He noticed that chicks would peck at a pictorial representation of grain with shadows and ignore real grain illuminated in such a way that shadows were eliminated. Hess (1950) found that chicks could be reared to peck at pictures of grain with the shadows pointing upwards, if their visual experience was

gained in an environment which was illuminated from below. Normally reared chicks always pecked at grain with downward directed shadows. Hess concluded that the chick not only makes use of the cues of light and shade for depth perception, but it is an acquired response dependent upon previous experience.

This conclusion presupposes that a chicken's preference for a particular photograph varies as a function of perceived depth. Twenty years later Hershberger (1970) trained chicks to discriminate convex from concave dents on the basis of primary cues alone. No illumination cues were present. When tested in extinction for preference to photographs in which illumination was the only cue, subjects always interpreted attached shadow orientation in terms of depth as though there were an overhead source of illumination. This occurred despite varied conditions of illumination during rearing. Hence, antithetical to the empiricism espoused by Hess (1950), Hershberger concluded that there appears to be an innate perceptual parameter corresponding to an 'overhead source of illumination' in terms of which orientation of attached shadow is interpreted as depth.

1.2.1 Relative Size

As an alternative to using instinctive motor responses, depth perception was also examined in terms of size constancy tests. Discrimination of distance is dependent on the size of the retinal image provided by an object, combined with past and present experience with objects of the same class. The reliance upon memory processes clearly demonstrates the higher order nature of this secondary cue to depth. Here retinal image size out of context is an unreliable cue to depth. It was generally regarded that an animal used some other cue to depth if it passed a size constancy test. This occurred when a

subject that had been trained to chose the larger of two identical stimuli, still continued to do so when the positive stimulus was displaced in depth such that the retinal image size of the two stimuli was equal.

Shinkman (1962) reported that both the carp (Herter, 1930, 1953) and the three-spined stickleback (Meesters, 1940) exhibit normal size constancy under binocular conditions, but failed monocularly. Size constancy has also been found in chicks (Gotz, 1926: see Gunter,1951), the bluejay (Hertz, 1928: see Shinkman, 1962) and chimpanzees (Kohler, 1915; Kluver, 1933: see Shinkman, 1962). Gotz comments:

> in spite of the inability to see stereognostically, hens reveal behaviour which allows us to conclude that they have an amazingly highly developed size constancy... (see Gunter, 1951).

These studies indicate that binocular cues to depth are necessary for size constancy. Implicit in this statement is the corollary that depth perception and hence size constancy is impossible under monocular conditions. However the cat, which also exhibited the size constancy phenomena with binocular vision, only failed to discriminate when made monocular for the test, while cats with 8 months of monocular experience learned to abstract the retinal image space appropriately (Gunter, 1951).

A problem in relating the size constancy studies to depth perception is that the animal is trained to pick the larger object rather than the nearer. A more direct approach came with the use of the visual cliff (Gibson & Walk, 1960). This apparatus evolved from studies using a jumping stand combined with a physical cliff. One of the earliest physical cliff studies was done by Yerkes (1904), who

measured the time taken by different species of turtles to step off a platform placed at various heights. He found that land turtles remained on the platform longer than water turtles while an amphibious species fell neatly in between! He interpreted this result as reflecting the evolutionary importance of depth discrimination for species of the same family which live in different environments. However, the amount of prior experience would have been a confounding factor. Kurke (1955) found that chicks jumped from a greater height than controls, if they were forcibly given experience of heights.

Jumping stand studies have been done primarily with rats. Russell (1932) found that the horizontal force exerted by an animal leaving a stand was a function of distance to a nearby platform. He observed that rats eyes seemed to converge before jumping, suggesting they were utilizing binocular convergence. However, with a full array of cues, monocular performance was almost as good as binocular. If all cues except retinal size were held constant, rats were unable to discriminate distance. In general, discrimination deteriorated the greater the number of cues that were eliminated. Greenhut and Young (1953) proposed that some of Russell's results were caused by serial order effects as they found that the force-distance relationship was not correlated if the distance was varied randomly rather than symmetrically as done in Russell's studies. However, this does not explain why the serial order effect was abolished if retinal size was the only available cue. Furthermore, in order to induce the animal to leap, Greenhut and Young administered electric shock and commented

> the animals were emotionally disturbed throughout the experiment, as indicated by their excretory - behavior and their resistance toward being put on the jumping platform

This alone was likely to destroy the correlation between force and distance.

The confounding of visual with non-visual stimuli was partly avoided with the visual cliff. This apparatus consisted of shallow and deep patterned sides divided centrally by a runway. Both sides were covered by clear glass at the level of the runway. Gibson and Walk (1960), and Walk and Gibson (1961) found that chicks, turtles, rats, lambs, goats, pigs, kittens, dogs and human infants all reliably chose the shallow side of the visual cliff after being placed on the runway. Tallarico (1961) observed a tendency for chicks to choose the shallow side as early as 3 hours after hatching. This was also the case with dark-reared chicks (Shinkman, 1962, 1963) or rats (Nealey & Edwards, 1960), indicating innate depth discrimination capabilities. Interestingly, if dark rearing was extended to 10 months of age, temporary deficits occurred (Nealey & Edwards, 1960).

The pattern on either side of the runway was usually checked squares. When the retinal image size of the checked pattern was made constant, both day-old chicks and adult rats still invariably chose the shallow side (Walk, 1965). If relative size was the only depth cue, day-old chicks were unable to choose one side over the other. This was not so with adult rats, who tended to choose the side with the larger pattern elements. An animal will descend from the centre board to a pattern in preference to a lack of pattern. Furthermore, if the visual cliff is made with a non-textured grey instead of the usual checked pattern, rats show no tendency to choose the shallow side (Gibson & Walk, 1960). Clearly the visual cliff discrimination is based on visual cues. It is also clear that relative size is a poor cue to depth in young chicks.

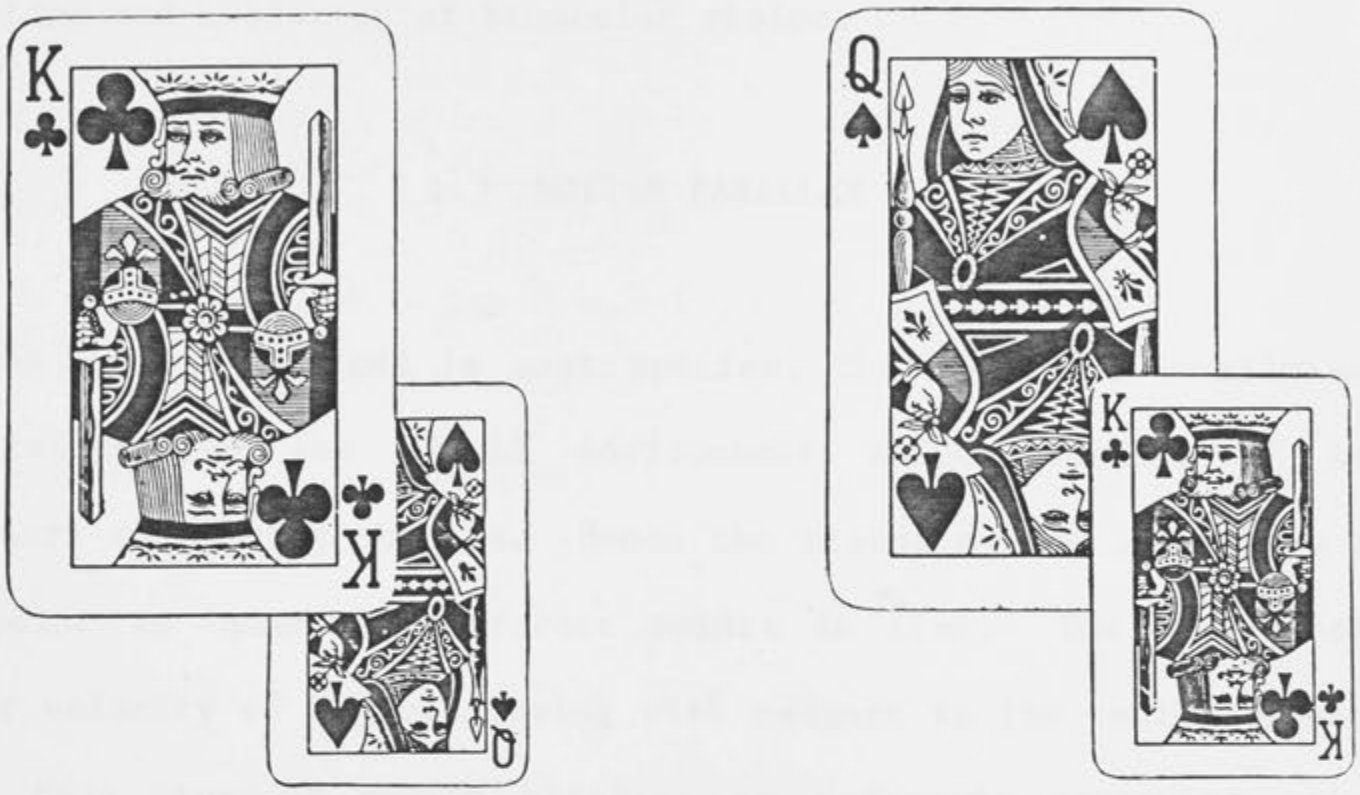
Insects too appear unable to judge distance on the basis of retinal image size (Wallace, 1959; Via, 1977). Gogel, Hartman and Harker (1957) have shown that in humans the retinal size of a familiar object is not an important cue to absolute distance. However under reduced cue conditions, the size constancy effect can be diminished to conditions closer to laws of visual angle alone (Holway & Boring, 1941). Hence, monocular human subjects show less inclination to abide by the laws of size constancy (Taylor & Boring, 1942).

Much of the data cited above implicates innate processes in depth perception. Combined with the apparent lack of use of the secondary monocular cues, particularly in young animals, one could conclude that to be effective they must be acquired through learning and experience.

1.2.3 Secondary Cues as Higher Order Stimulus Variables

Ames (see Ittelson, 1968) formulated a striking demonstration of the influence of past experience in humans on the secondary monocular cue of interposition (the cue of interposition occurs when an overlapping object is said to be nearer than an overlapped object). Ames demonstrated that a false interposition cue could over-rule spatial information derived from other cues and reverse the real depth relationship based on the subject's past experience (see Figure 1.1). Processes of this sort are of the kind that von Helmholtz (1867) described as unconscious inference.

The secondary monocular cues to depth are by definition, two dimensional cues to three dimensional space. Thus each pictorial cue produces an optic array that is shared by an entire family of three-dimensional arrangements. In order to resolve the ambiguity implicit in each cue alone, the spatial attributes of form perception must consider the orientations and spatial relationships between the various objects in the field of view (Bishop & Henry, 1971).



A B

Figure 1.1 A. King is placed in front of Queen. B. Then the subject views the Queen, in which the bottom right hand corner is removed, placed in front of the King. Subject reports he sees a small King in front of the Queen, rather than a normally sized King behind the Queen.

In considering these relationships, the visual system must resort to memory processes, thus placing the secondary monocular cues to depth within the category of higher order stimulus variables. Such a categorization represents the structuralist tradition in which perception consists of underlying fundamental sensations and their physiological bases, and the laws by which these elements combine. Most current research, particularly influenced by the upsurge in neurophysiology, has thus been examining the 'fundamental sensations', and higher order stimulus variables have largely remained unattended.

The three dynamic areas of depth perception revolve around the cues motion parallax, accommodation, convergence and stereopsis. The latter two have been accompanied by a growing interest in the mechanisms and evolution of binocular vision.

1.3 MOTION PARALLAX

The head, body, and in most species, the eyes, continually move with respect to the visual environment which consists of both stationary and moving objects. Hence the visual system may sample the same point in space at different points in time. The differential angular velocity of objects moving with respect to the retina or vice-versa, thus provides motion parallax as a dynamic monocular cue to depth.

Von Helmholtz (1867) emphasized the importance and effectiveness of motion parallax in comparison with other depth cues:

> Suppose for instance, that a person is standing still in a thick wood, where it is impossible for him to distinguish, except vaguely and roughly, in the mass of foliage and branches all around him what belongs to one tree and what to another....But the moment he begins to move forward, everything disentangles itself (p 296).

Yet most early human studies have failed to show that motion parallax in isolation is an effective cue to depth. If one simulates the transformations that would be produced by a surface tilted in depth, subjects either do not report a consistent impression of relative depth or slant (Gibson & Carel, 1952), or they produce estimates which vary widely (Gibson *et al.*, 1959). Epstein and Park (1964) and Gogel (1977) both put forward the view that motion parallax is not truly

effective in isolation as an exocentric due to depth. Gogel & Tietz (1973) in examining the specific distance tendency, found that head motion only provides cues to distance by allowing perceptual learning.

In contrast to these studies, Eriksson (1974) studied successive discrimination on the basis of motion parallax where the observer moved his head, and found that perceived distance increased with target distance in the range of 2-4 metres. Johansson (1972: see Foley, 1978) also found that accurate discrimination based upon motion parallax co-varied with accommodation over distances of 30-240 cm.

Perhaps the clearest evidence for the effectiveness of motion parallax comes from studies which have used complex or information-rich stimulus displays. Rogers and Graham (1979) used a random dot display that could be transformed by each movement of the observer or the display oscilloscope. As soon as the observer's head was moved, relative movement was generated between the elements (dots) which matched the motion parallax produced by a real three dimensional surface. This produced consistent and unambiguous impressions of relative depth not unlike that found with stereopsis. The relative motion of the rows of dots was not perceived. Thus, Rogers and Graham conclude that motion parallax provides an accurate and unambiguous source of information about the depth of objects. Other authors, notably Braunstein (1976) have come to similar conclusions. Ullman (1979) has shown mathematically that there is sufficient information in a sequence of only 3 discrete views of 4 points to uniquely specify the three dimensional surface structure of any rigidly moving surface.

Unlike stereoscoic vision, monocular movement parallax provides conditions for depth perception with movement along any axis, not only the horizontal axes. J.J. Gibson (1950) pointed out that motion parallax in the traditional sense is only one of a number of

transformations. Other retinal transformations include the optical expansion patterns produced by movement through the visual world and the patterns of retinal change produced by object rotation (Gibson, 1966; Braunstein, 1976). Hence for motion parallax to be effective in a complex visual world, either the objects or the observer may move in any direction. However, the threshold sensitivity for motion parallax in humans is not equal for all directions. It is best for horizontal and worst for vertical axes of movement (Graham, 1965). Nor is this effect due to binocular motion in depth cells tuned in the horizontal plane (Cynader & Regan, 1978) as the thresholds were measured monocularly. It may reflect differences in retinal gradients along the various foveal-peripheral axes.

Only a handful of studies have directly examined motion parallax as a cue to depth in animals, although it has frequently been implicated by observations such as head bobbing in birds (Grinnel, 1921; Pumphrey, 1948: see Shinkman, 1962) and peering behaviour in insects (Wallace, 1959). Walk (1965) describes experiments of Schiffman (1961) and Trychin (1962) who found that both chicks and rats chose the shallow side of the visual cliff under monocular conditions with no relative size cues present. Furthermore this discrimination fails if only one pattern element is present, indicating that accommodation is not operative. Addition of elements increased the probability of discrimination, and peering movements implied the possible use of motion parallax information.

A more direct study of motion parallax in relation to peering behaviour was done with the locust (Collett, 1978). This study revealed that the angular orientation of the locust head remained constant, and amplitude of peering increased with greater object distance, which to some extent enables compensation for the inherent

decline in accuracy with distance (Horridge, 1977). Collett concludes that, provided the locust knows how far (or fast) it moves its head, it can measure image displacement (or velocity) and thus compute the distance of the object. This, however, is not synonymous with motion parallax seen in the human situation as it simply allows egocentric distance estimation, rather than relative distances (i.e. depth) between objects to be measured. Discrimination of movement is, however, a necessary prerequisite for detection of the differential angular velocity.

The importance of movement as a visual stimulus is apparent across species. An early review of motion sensitivity can be found in Kennedy (1936). Not only amphibians, but most snakes, lizards, and many carnivorous turtles do not respond to motionless prey. Walls (1942) recognized that the successful use of the habit of 'freezing' is in itself an evidence that the predator does not identify them as well visually.

Birds too seem to easily detect movement. An eagle can see moving prey at great distances. It is often reported that a homing pigeon can detect a moving hawk well in advance of any human observer. It has even been postulated that the avian optical structure, the pecten, accentuates this motion sensitivity by the creation of a stroboscopic shadow on the retina (Menner, 1938, see Walls, 1942, p.365).

Physiological evidence has shown that neurones respond preferentially to moving contours at almost every level of the pigeon visual system (Maturana & Frenk, 1963; Jassik-Gerschenfeld *et al.*, 1970), yet the least detectable stimulus velocities from psychophysical studies in the pigeon are surprisingly high and readily detected by humans (Hodos, Smith & Bonbright, 1975).

Accurate apparent movement detection has been shown in the pigeon (Siegel, 1970), although stimulus control may have been achieved by illumination change on a local area of the rotating disc, rather than by the apparent movement of an entire pattern. A thorough study by Hodos, Smith and Bonbright (1975) measured absolute thresholds for detecting movement of a grating stimulus. The threshold was found to be 4-6°/sec. and is well above the human threshold which is of the order of 0.4-6.0 min/sec (Brown, 1931; Leibowitz, 1955).

Neither absolute nor apparent movement detection implies that the pigeon uses motion parallax as a cue to depth. Perhaps closer to the mechanism underlying motion parallax is differential motion sensitivity. Mulvanny (1978) reports that the thresholds for differential motion sensitivity are only 10-12°/sec. Whether relative velocity detection is used to estimate the depth of objects, however, is open to debate. It remains clear, that in the frontal visual field, motion sensitivity measured by various means, appears relatively poor.

Detection of movement is not confined to central vision. The extreme periphery will discern a wriggling finger without knowledge of the brightness, colour or form of the finger. Clearly, peripheral movements have a saliency and attention value across species, quite out of proportion to the clarity with which they are actually discriminated.

Of interest is a study by Martinoya *et al.* (1983) who examined absolute motion sensitivity in both the frontal and lateral visual fields of the pigeon. The pigeon has often been described as myopic in the frontal field, and hyperoptic in the lateral fields (Catania, 1964; Millodot & Blough, 1971), thus allowing observation of food while pecking, and the ability to detect the movement of possible

predators with lateral regard (Catania, 1964; Goodale, 1983b; Bloch & Martinoya, 1983). Martinoya *et al.* (1983) trained pigeons to discriminate the direction of moving square wave gratings presented tachistoscopically. The stimuli were presented at 40cm, in either the frontal binocular or lateral visuals fields. For frontal viewing the threshold was similar to that found by Hodos, Smith and Bonbright (1975), but the lateral thresholds were in the range 1.4 - 2.5°/sec. Hence, the lateral sensitivity to motion was some three times better than that seen in the frontal field.

It could be argued that the difference between the two visual fields was due to the fact that the moving gratings presented in the frontal field were horizontal and moved downwards, while for the lateral presentations, the grid was projected vertically and moved backwards. Although consistent with the optic flow while flying, the patterns of movement were stimulating the retina in orthogonal directions. Recall that motion parallax in humans varies as a function of the axis of movement. The superiority of lateral motion sensitivity may arise at the level of the retina. It is known that in the cat, Y-cells are prevalent in the peripheral retina. These cells are responsive to fast target movements, and may well analyse temporal patterns (Sherman, 1982). Similar mechanisms may exist in the pigeon, although the lateral superiority to motion detection may arise at subsequent stages in the visual system.

It has been found very difficult (Bloch & Maturana, 1971) if not impossible (Catania, 1963) to train pigeons with a lateral presentation of a form discrimination. Nye (1973) reports that the pigeons' ability to discriminate colour, form, brightness and moving patterns diminished as the stimuli progressed in the lateral direction. He concludes that it is difficult for the pigeon to

develop a direct associative pecking response to laterally located stimuli. This clearly contradicts the results from Martinoya *et al.* (1983). Furthermore, Nye's hypothesis cannot be entirely correct as laterally presented colour stimuli can be readily associated with pecking in the pigeon (Bloch & Maturana, 1971).

1.4 OCULOMOTOR CUES

1.4.1 Accommodation

The process by which the refractive power of the eyes is altered to ensure a clear retinal image is known as accommodation. Points nearer or further than the fixated point produce blur circles which vary as a function of distance between the point and the fixated point (Southall, 1937). Discrimination of depth based on accommodation alone was first reported by Wundt (1862, see Foley, 1978) and later by Le Grand (1967). Their subjects viewed through a tube a thread against a bright background, but possible artifacts such as would have arisen if the eye, tube and thread positions were not in alignment were never eliminated. Subsequent investigators have found no relationship between perceived distance and accommodation (Heinemann *et al.*, 1959), ordinal (Woodworth, 1938; Biersdorf, 1966) or a non-linear relationship (Gogel & Tietz, 1973; Foley, 1977). Hence, while accommodation may serve as a cue to depth in humans, it is severely limited in its capacity to do this. It is neither precise nor accurate over distances greater than a metre or so (Baird, 1903; Graham, 1965).

1.4.2 The Relationship between Accommodation and Convergence

The change in the relative positions of the visual axes is called convergence when the angle formed by the axes increases, and divergence when this angle decreases. The synkinesis between accommodation and convergence plays an important physiological role in binocular vision in near fixation. Whenever a person exerts a certain amount of accommodation, a determined amount of convergence is elicited. The reverse also seems to hold (Finchan & Walton, 1957). Convergence so elicited is expressed clinically as the accommodation/convergence ratio (Fry, 1939; Fry & Haines, 1940). Accommodative convergence provides the gross adjustment for the position of the eyes, but acting alone it rarely, if ever, provides binocular single vision. Fine adjustment is obtained by fusional convergence (see Von Noorden, 1980) and is elicited by disparate retinal stimuli.

Owens (1974, quoted in Foley, 1978) has shown that the resting state of convergence is more closely related to perceived distance in the absence of information, than is the state of accommodation. Here there is an interdependence between the depth signal in the absence of distance information, and the oculomotor state. Discrimination based on convergence alone appears to fail when the stimuli are such as to create the impression that they are physically identical (Foley, 1978). This is due, perhaps, to the conflict between size constancy and convergence. Other studies have implicated convergence as an independent cue to distance (Swenson, 1932; Foley & Held, 1972).

1.4.3 Accommodation and Depth Perception in Animals

Homatropine has been used to abolish accommodation in kittens (Walk, 1965) and curare has been used for the same purpose in chicks (Shinkman, 1963), but there is no resultant impairment in performance on the visual cliff. Nealey (in work discussed by Shinkman, 1962) projected a blurred or a clear pattern of equal size onto both sides of the visual cliff at equal depth and found that rats showed no preference for either side. Due to non specific drug effects and indirect modification of accommodative depth cues, these studies can hardly be proclaimed to support the notion that accommodation was not used for the perception of depth.

Ingle (1968, 1972) measured the snapping response of frogs and toads. He found that estimation of distance to prey was done as well with one eye as with two, and proposed that the animals do this by monitoring the accommodative state of their eyes when the prey is in optimum focus. The chameleon has also been proposed to use a similar mechanism for depth localization (Harkness, 1977). This reptile has a central fovea with extensive independent voluntary eye movements. Walls (1962) describes:

> their total lack of binocular conjugation, are all made conveniently conspicuous by the fact that the creature's high eye bulges prominently and has the lids permanently fused with its surface... (p. 75).

Harkness found that binocular and monocular chameleons perceived prey distance as some function of the plane of focus, and accommodation was not just used as a back-up cue when binocular information was unavailable.

1.5 STEREOPSIS

Wheatstone's invention of the stereoscope in 1838 revealed that the basis of stereopsis is binocular disparity due to the horizontal parallax shift between corresponding points on the left and right retinas.

1.5.1 The Horopter

Vieth (1818) first geometrically specified that points seen binocularly as single in the horizontal plane of the fixation point should lie on a circle that passes through the fixation point and the optical centres of the two eyes. The geometrical construction became known as the Vieth-Muller circle (Muller, 1826, see Boring, 1942). Thus in Figure 1.2, points X, Y and Z are on the horopter and are said to stimulate corresponding retinal points.

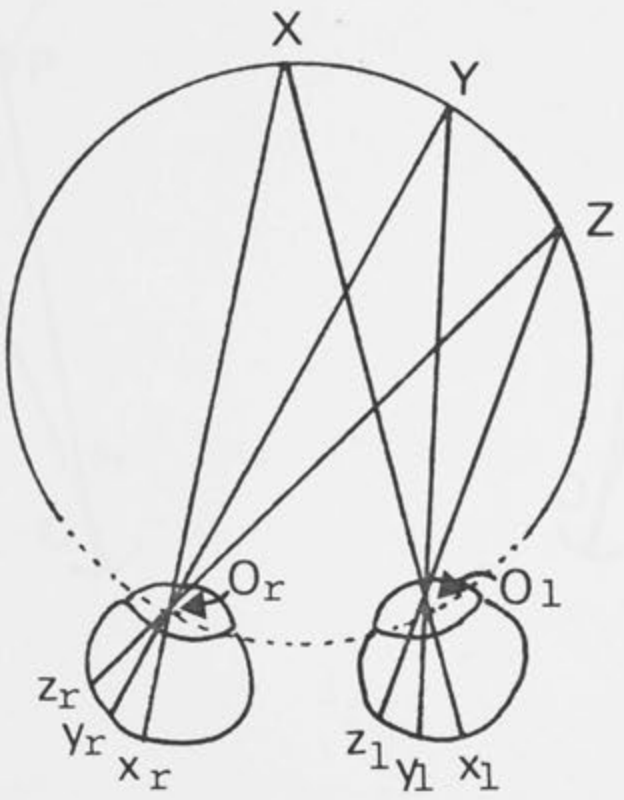


Figure 1.2 The Vieth-Muller horopter circle. X_r and X_l are corresponding points. Similarly for Y_r and Y_l and Z_r and Z_l. 0, optical centre.

Von Helmholtz (1867, translated 1925) and Hering (1879, translated 1942) realised that the Vieth-Muller circle was an oversimplification, and worked out forms of a general horopter based mainly on the determination of the apparent frontoparallel plane. The variety of criteria that have subsequently been proposed as a basis for the horopter (Ogle, 1962; Shipley & Rowlings, 1970) testify to the fact that the concept of the horopter has yet to find a clearly defined place in the theory of binocular vision. Bishop (1981) suggests that the horopter may best be considered as the zero-disparity reference plane that contains the fixation point and relative to which stereoscopic depth estimates are made.

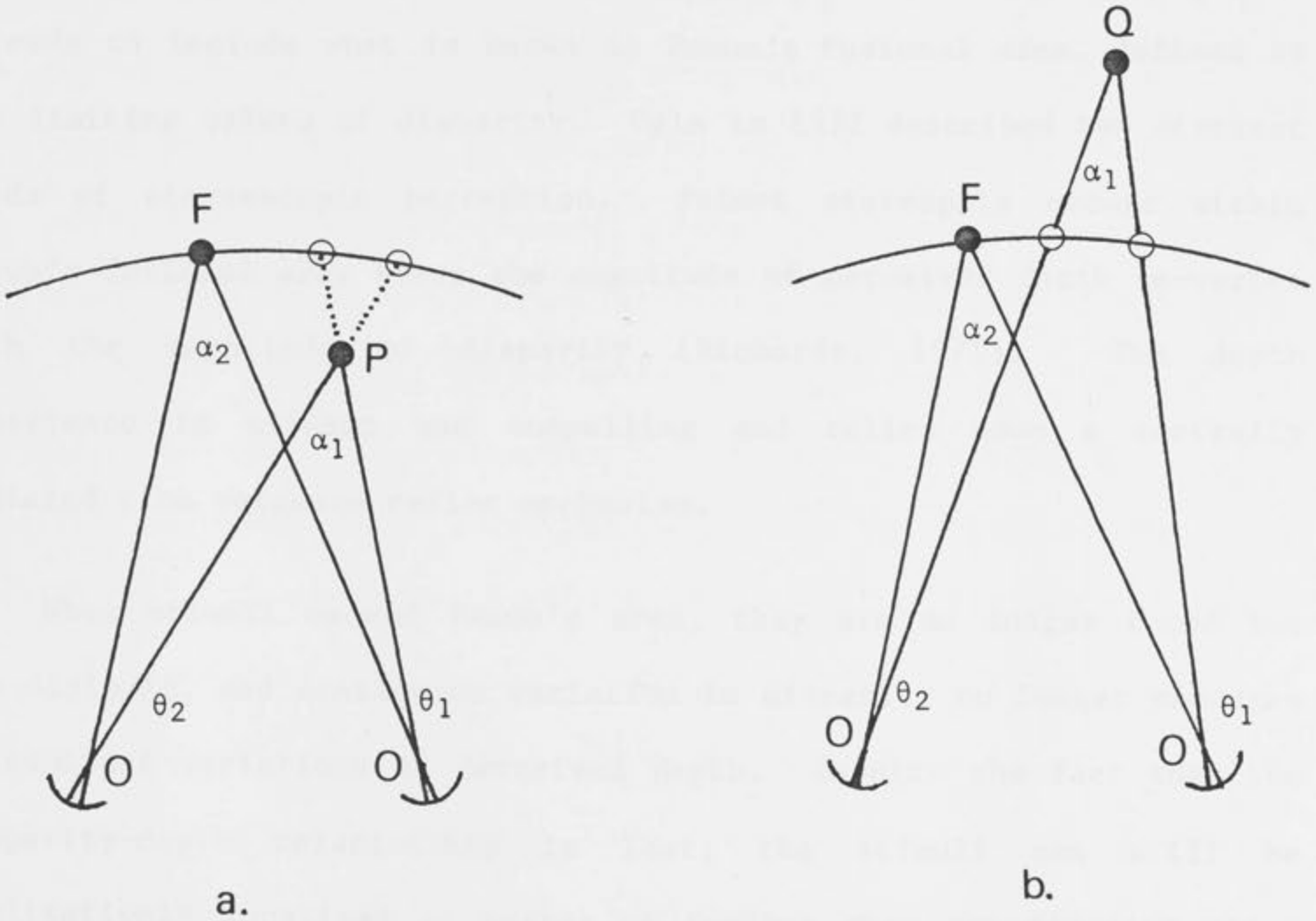


Figure 1.3 Physiologic diplopia. a. Crossed disparity of the object P, closer than the fixation point F. b. Uncrossed disparity of the object P, more distant than the fixation point. O, optical centres; $\theta_2 - \theta_1 = \alpha_1 - \alpha_2$, retinal disparity.

An object nearer (P) or further (Q) (within limits) from the fixation point (F) in Figure 1.3, will produce crossed or uncrossed disparity, respectively, by virtue of the relative horizontal disparity between the retinal points which do not exactly correspond. Thus, the difference between the visual angles θ_2 and θ_1 defines the relative disparity between points F and P, or F and Q, and leads to the stereoscopic perception of P or Q appearing to lie in depth relative to F. Notice that only horizontal, not vertical disparities give rise to stereopsis.

1.5.2 Spatial range of stereopsis and the distinction between fine and course mechanisms.

Binocular vision is not limited to points on the horopter but extends to include what is known as Panum's fusional area, defined by the limiting values of disparity. Ogle in 1952 described two distinct kinds of stereoscopic perception. Patent stereopsis occurs within Panum's fusional area where the magnitude of perceived depth co-varies with the magnitude of disparity (Richards, 1971). The depth experience is evident and compelling and relies upon a centrally mediated fine vergence reflex mechanism.

When stimuli exceed Panum's area, they are no longer fused but are diplopic, and continuous variation in disparity no longer produces concomitant variations in perceived depth. Despite the fact that the disparity-depth relationship is lost, the stimuli can still be qualitatively localized as nearer or further than the fixation point (Westheimer & Mitchell, 1969; Mitchell & O'Hagen, 1972). Ogle referred to the stereoscopic perception of diplopic stimuli as quantitative stereopsis. Similarity of the two retinal images is not a necessary requirement (Mitchell, 1969, 1970). Qualitative

stereopsis has associated with it a peripheral coarse stereopsis and fusional mechanism. Fine single vision is always accompanied by coarse fusion.

Tests for Stereopsis

Wheatstone's stereoscope is an example of a haploscopic device in which separate two-dimensional targets (in this case by way of mirrors) are presented to each of the two eyes.

Subsequent investigators examining stereoscopic acuity and factors influencing stereopsis have used real depth instruments. The classic example is the Howard-Dolman apparatus (Howard, 1919) in which two vertical rods, one stationary and the other moveable, are viewed through an aperture against a luminated background. The subject can then adjust the moveable rod until aligned and side by side with the stationary rod. Although it is conceivable that retinal image size may mediate the discrimination, Howard showed that monocular thresholds were 20 times as great as thresholds obtained on the basis of binocular vision. As measurements were made outside the range of effective convergence, this apparatus relies on the cue of retinal disparity for successful discrimination. Our own observations on a group of 30 students revealed that motion parallax obtained by lateral head movement could aid monocular discrimination such that error of alignment was reduced by half (from a mean of 63.6cm to 30.4cm). Binocular performance, however, was always superior to monocular performance (McFadden & Gillette, 1982, unpublished observations). A variation of the Howard-Dolman apparatus is the Verhoeff stereopter where vertical wires replace the rods. This reduces possible contamination by retinal size cues.

In clinical testing of stereoacuity haploscopic devices are normally used. Examples are the Titmus, Wirt, T.N.O. and Reinecke E Test. Separate images are presented to each eye by the use of red and green filters worn over each eye and matched to each of the two coloured images, or polarized goggles in which the vectographs are so imprinted that each target is polarized at 90 degrees with respect to the other (see Hinchliffe, 1978).

1.5.4 Local and Global Stereopsis

Julesz (1960) was the first to consider the use of computer-generated random dot arrays to produce a stereogram in which each target appears as a homogeneous random array of small squares or elements (dots) without any global shape or contour visible. Retinal disparity, defining the configuration of a particular form, is produced by laterally displacing a subset of dots in one matrix relative to corresponding dots in the other matrix. In such random dot stereograms (RDS), if the horizontal shift is always kept an integral multiple of the cell size, then no cell of the background will ever be partly covered by the shifted areas, and thus no monocular cue will be present.

When the target components of the RDS are binocularly fused, the particular form that is displaced 'jumps out' in vivid depth above the background. In order for this to occur retinal corresponding points must be identified. Since in a RDS any local dot in one field can be matched by many neighbouring identical dots in the other field, many false localizations may occur (Figure 1.4). The ambiguity can be solved by pooling several adjacent dots that have similar binocular disparities and perhaps some other feature in common. The search for a unique solution that yields the densest (maximum) correlation in

certain areas is the essence of global stereopsis. Since the visual system manages to overcome this ambiguity and arrive at the correct global solution in a RDS, Julesz has effectively shown that global stereopsis can occur in the absence of any monocular form or other depth cues.

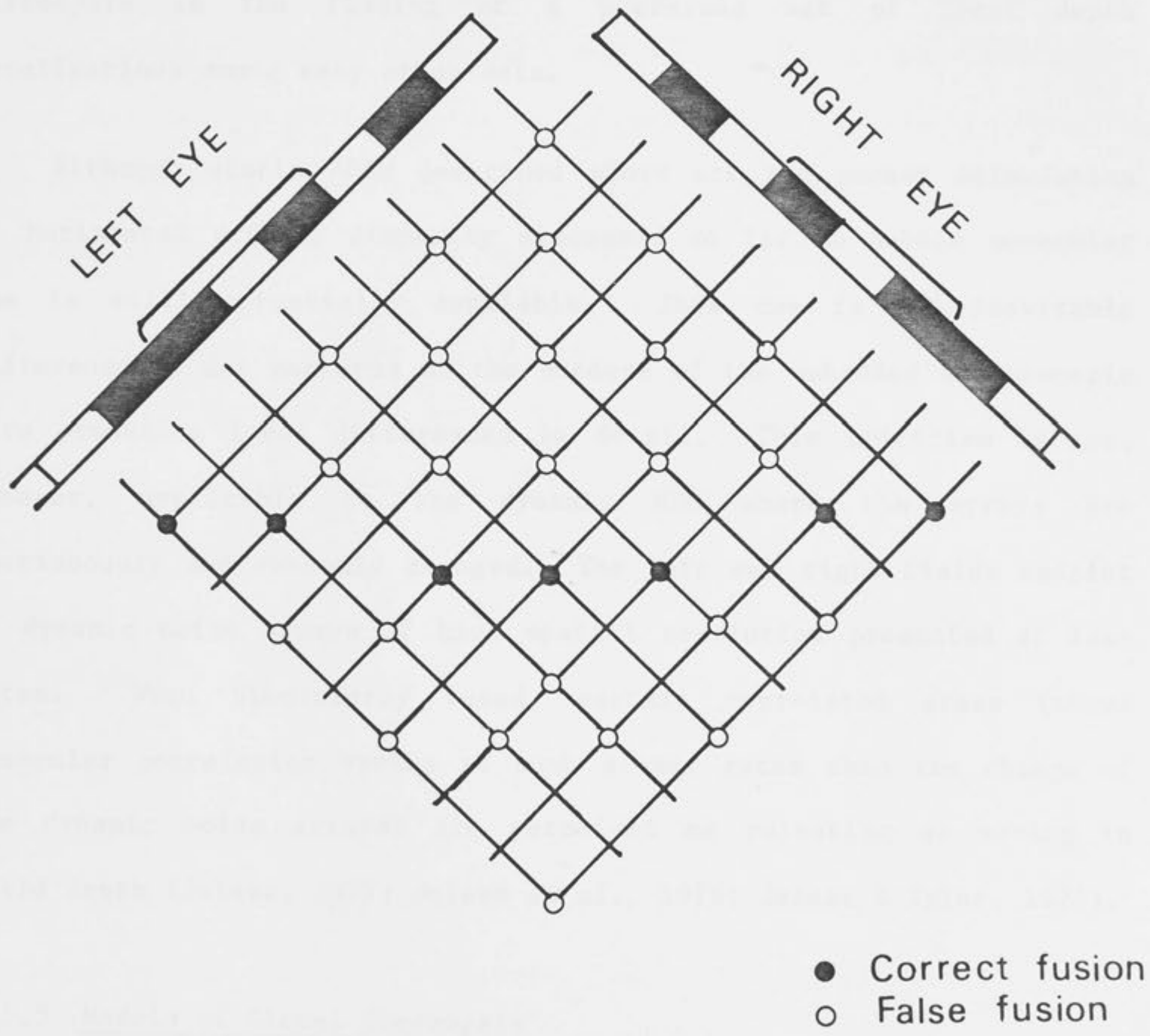


Figure 1.4 Illustration of how false localizations of targets occur, thus creating ambiguity in global stereopsis.

For classical stereograms (Ogle, 1962; Richards, 1971), either with a few elements or monocular labels, there is no ambiguity of corresponding retinal projections. Such a process of unambiguous depth localization is called local stereopsis. It operates on feature elements such as dots, lines, edges or corners, and each feature pair is assigned a depth value relative to the fixation point. Local stereopsis is defined as depth localization (on the basis of binocular disparity alone) of elements whose correspondence (and thus binocular disparity between them) can be unambiguously established. Global stereopsis is the finding of a preferred set of local depth localizations among many other sets.

Although static RDSs described above are the purest stimulation of horizontal retinal disparity discussed so far, a subtle monocular cue is still potentially available. This cue is the inevitable difference in dot patterns at the borders of the embedded stereoscopic form producing local differences in detail. This criticism is not, however, applicable to the dynamic RDS where the arrays are continuously and randomly changed. The left and right fields consist of dynamic noise arrays of high spatial resolution presented at fast rates. When binocularly fused, certain correlated areas (whose binocular correlation varies at much slower rates than the change of the dynamic noise arrays) are perceived as pulsating or moving in vivid depth (Julesz, 1971; Julesz *et al.*, 1976; Julesz & Tyler, 1976).

1.5.5 Models of Global Stereopsis

Several groups of investigators are actively engaged in efforts to model global stereopsis (e.g. Julesz & Chang, 1976; Marr & Poggio, 1979; Mayhew & Frisby, 1980). In the classic literature (e.g. Ogle, 1959) there has been a tendency to regard the limit of Panum's

fusional area as fixed. However, this is not the case with global stereopsis. The elastic nature of Panum's area became apparent with the discovery of hysteresis. Here, under binocular retinal stabilization, after a RDS of foveal size is brought within 6 min of arc alignment, it can be slowly pulled apart by as much as 120 min of arc without losing fusion (Fender & Julesz, 1967; Burt & Julesz, 1979; Hyson *et al.*, 1980). The more dots a RDS contains, the larger the hysteresis effect, thus suggesting cooperative processes at work.

Another temporal process operating over a much longer time scale occurs, where extended exposure increases the magnitude of disparity that observers perceive as fused (Julesz, 1971). The magnitude of the maximum disparity increases with square root increases in area of the stereoscopic form (Tyler & Julesz, 1980).

The cooperativity of global stereopsis has been further demonstrated by Julesz & Chang (1976) who showed that the global state of an ambiguous RDS (that had a target either in front or behind the surround) could be consistently pulled by a small bias towards one of the global states. They argue that this effect supports a parallel rather than a serial model of stereopsis.

In order to create ambiguity in the relation between depth and disparity (Blakemore & Julesz, 1971), two detectors must signal the same depth even though they respond optimally to entirely different regions of the disparity spectrum. One possible mechanism would be to create a pool of different disparity detectors, the total activity of which would be the correlate of the magnitude of the depth sensation. Richards (1971) finds that some people can make normal depth matches to crossed disparities, while failing to distinguish uncrossed disparities, or vice-versa. Based on his clinical findings he distinguishes three pools of binocular activity: crossed, near zero

(confuse sign) or uncrossed disparities.

Theoretical formulations of stereopsis have been questioned on the grounds that they fail to incorporate the phenomenon of stereoscopic depth constancy, in which for a constant disparity, perceived depth increases with perceived distance (Gogel, 1961; Wallach & Zuckerman, 1963; Foley, 1967; Ono & Comerford, 1977). Foley (1972) outlines a model by which neuronal disparity outputs would be modulated by information derived from convergence eye movements. Thus, Foley abandons the relative distance invariance hypothesis proposed by investigators who believed that the visual system could not extract information about egocentric distance from convergence (Blank, 1953, 1958; Hardy *et al.*, 1953). Foley's model requires that perceived depth, as originally proposed by von Helmholtz (1867, translated 1925) depends not only upon disparity, but also on the perceived egocentric distance of one of the targets. This is true only for small disparities less than four degrees (Foley, 1978). The reverse, however, cannot be argued to be true - that perceived egocentric distance depends upon disparity. This point will be reviewed in the section on stereopsis in insects.

1.5.6 Neural Mechanisms

Barlow, Blakemore and Pettigrew (1967), Nikara, Bishop and Pettigrew (1968) and Pettigrew, Nikara and Bishop (1968) were the first to describe a group of cells in the cat visual cortex that respond selectively to horizontally disparate stimulation of the two retinas. Cells sensitive to binocular depth have also been found in the macaque monkey (Hubel & Wiesel, 1970; Poggio & Fischer, 1977), the goat (Clarke & Whitteridge, 1976a) and in some predatory birds (Pettigrew and Konishi, 1976; Pettigrew, 1979).

Because of the small size of the receptive fields, especially in the centre of gaze, the binocular depth estimates must be based on very localized features of the two retinal images. Binocular single vision occurs because both receptive fields report the same stimulus feature at the one locus, when the two receptive fields are accurately aligned. At depths closer or further away from this site, the two receptive fields are slightly out of register. It is suggested, based on the study of simple cell organisation (Bishop and Henry, 1971) that the marked mutual inhibition between the two receptive fields prevents double vision within Panum's fusional area. Outside this local area the possibility of double vision arises because the receptive fields act independently.

Four types of depth sensitive cells have been found in both Areas 17 and 18 of the alert behaving macaque monkey (Poggio & Fischer, 1977). Fine stereopsis appears to be supported by the properties of the tuned excitatory and inhibitory neurones, while near and far cells that responded over a much wider range of depth could operate as part of a coarse stereopsis mechanism. These orientation and disparity sensitive local stereocells can thus serve as the neural substrate of a local stereoscopic mechanism.

Global stereo units could also exist one hierarchical level above the local cells. The existence of a complex stereo unit in the cat cortex has been reported by Blakemore (see Julesz, 1971). In addition to the binocular columns in Area 17 that contained edge detectors firing for the same binocular disparities, there was another columnar organization. These latter columnar modules contained overlapping contralateral receptive fields while the ipsilateral receptive fields varied greatly in their locations. Blakemore suggests that depth localization is accomplished by the depth columns (disparity units)

while positioning is performed by the direction of columns.

There is also evidence that position in depth is processed by a different population of cortical neurones than motion in depth (see Bishop, 1980).

1.5.7 Behavioural Demonstrations of Stereopsis in Animals

Despite the wealth of psychophysical literature on stereopsis in humans and neurophysiology thereof in cats and monkeys, there are very few behavioural demonstrations of stereopsis in animals.

1.5.7.1 *Cats*

Stereopsis was first behaviourally demonstrated in the cat (Fox & Blake, 1971) using disparate stimuli presented by the shadow-casting technique. A cat was firstly trained to discriminate between a centre rod placed behind or in front of two side rods. The learning paradigm employed was conditioned suppression of a lick response for food reinforcement. Once this discrimination had been mastered, transfer was immediately obtained from the real depth situation to a stereoscopic presentation in which two disparate coloured shadows of each of the three rods were cast onto a screen and viewed via anaglyphic colour filters. Fox & Blake also noted that motion parallax, as indicated by head movement or systematic eye closure, was not used. Since transfer from the physical to the stereoscopic contours was easily obtained, they concluded that the discrimination of crossed from uncrossed disparity was indeed based upon stereopsis.

Using the same technique, Packwood and Gordon (1975) found that cats that were deficient in binocular cortical neurones - either by being raised with alternating monocular vision, or being Siamese and hence possessing an aberrant genetically determined geniculostriate pathway - failed to learn the stereoscopic discrimination.

Performance on the physical contour depth task, visual acuity, and photopic sensitivity remained normal. Hence, binocular cortical neurones appear to be essential for normal stereoscopic function. It is interesting that these cats learnt the real depth task on the basis of monocular cues, at the same rate (within 240 trials) as normal binocular cats. Thus it would seem unlikely that stereopsis would completely overshadow the other monocular cues in normal animals.

In all these studies, the minimum disparity difference was large (1°). The strength of the stereoscopic cue would clearly be enhanced at threshold levels of testing. Blake and Hirsch (1975), found that the threshold for detecting rod displacement in cats was 4 min of arc under binocular conditions, while for monocular cats, the threshold was increased by a factor of ten.

A very elegant study presenting a compelling case for the presence of stereopsis in cats, was done using dynamic RDS produced in red and green anaglyphs (Lehmkuhle & Fox, 1977). The same learning paradigm as in the previous studies was used and again transfer was found from the physical to the stereoscopic stimulus. Interestingly, although perhaps not surprising, cats could detect a change in the orientation of the stereoscopic form.

In order to investigate develomental changes, a faster but less sophisticated method of assessing stereoscopic status in cats was developed by Mitchell *et al*. (1976) and Mitchell, Giffen & Timney (1977). This was based on the jumping stand of Lashley (1930, 1931). Cats were induced to leap to the nearer of two platforms patterned with a range of different sized dots. The threshold disparity corresponding to the smallest discriminable depth difference was approximately 4 min of arc for binocular conditions. Monocular viewing consistently resulted in inferior performance, although given

a sufficient number of trials (several months), performance improved. This indicates that cats can employ extemely subtle monocular cues to depth such as relative dot density, size differences and/or brightness cues.

Using a similar technique, Kaye, Mitchell & Cynader (1982) found that dark rearing of cats resulted in reduction of binocular thresholds to monocular levels. These animals were also found to have a reduced complement of binocularly influenced cortical neurones. Thus it would seem that cats possess functional stereoscopic capabilities, provided the binocular system is not impaired as defined either anatomically or electrophysiologically.

1.5.7.2 *Meerkat*

The use of binocular depth cues has also been claimed in the meerkat, a diurnal social carnivore with extensive binocular overlap (Moran *et al.*, 1983). Again using the jumping stand technique modernized by Mitchell *et al.* (1976), they measured binocular and monocular depth thresholds. The threshold, defined where the psychophysical function crossed the 70% correct line, was estimated to be 10 min of arc for binocular viewing and unattainable for subsequent monocular conditions. However, it was not indicated how long monocular training was pursued, although it was noted that monocular performance improved markedly when the edge masker was removed. This produced monocular depth cues such as interposition and a perspective view of the whole apparatus. They conclude that the meerkat's superior binocular performance was due to the use of retinal disparity. Although the conclusion is quite probable, the data leave open two questions. Firstly, does convergence mediate the discrimination, and secondly, will occlusion of one eye affect performance on a non-depth discrimination?

1.5.7.3 *Primates*

Stereopsis has also been demonstrated behaviourally in monkeys. Bough (1970) used static RDS conveyed to each eye by polarized goggles. Two macaque monkeys were first trained using a fading procedure with a form cue to distinguish between no disparity present from a RDS in which binocular disparity produced an inner square behind the plane of the surround. The monkeys were also able to distinguish convergent from divergent disparity. Chance performance on the discrimination was produced by occlusion of one eye or by artificially produced convergent strabismus, although these controls were tested for only one session.

Evidence for global stereopsis in the rhesus monkey was found by substituting the dichoptic polarization system with chromatic filters of complementary wavelength (Cowey *et al.*, 1975). These authors reported that the polarization system was abandoned as they found brightness cues were present due to the dependence of the polarization angle with head tilt. Again with static RDS, Harwerth & Boltz (1977a, b) describe an investigation of the effect of exposure duration on stereopsis in rhesus monkeys in which impairment of performance was observed as duration decreased. With static RDS, a subset of matrix elements creating the stereoscopic form(s) must be off-set by an integral number of elements to avoid monocular cues. Therefore, the smallest disparity that could be produced in this study was 6 min of arc - well above the minimum stereo threshold for local stereopsis of either humans or monkeys with unrestricted viewing.

The threshold for resolving disparity in the monkey was investigated by Sarmiento (1975), who used a classic two-contour discrimination task and determined the smallest difference in depth between two rods that the animals could discriminate. The threshold

disparity angle for the one monkey completing training was 2-4 sec of arc. This occurred at the highest background luminance tested (1.5 log mLamberts). At this same luminance, the best of six human observers was 2.3 and 2.5 sec of arc. The relationship between stereoacuity and luminance was also similar in monkeys and humans. With the real depth stimuli used, two cues to depth are present in addition to binocular disparity - retinal image size and motion parallax. Differences in retinal image size were small and it is known that when they are the only cues, thresholds are from 5-20 times greater than those based on stereo cues (Howard, 1919; Sloan & Altman, 1954). Thus good resolution in depth was itself an indication that binocular disparity was utilized.

Dynamic RDS have been used with monkeys by Julesz, Petrig & Buttner (1976). Again tests were made of transfer from real to stereoscopic stimulus presentation. Taken together, there seems to be no room for doubt about the existence of stereopsis in the monkey.

1.5.8 Stereopsis in Non-mammals

The visual system of mammals (especially primates) includes frontal placement of the eyes, yoked eye movements, and the partial decussation of the optic tract which permits corresponding retinal areas to combine at the same cortical sites. The visual system of most non-mammals is characterized by more laterally placed eyes, which, in some species can move independently of each other (e.g. the chameleon), and by complete decussation of the optic tract.

These differences between the mammalian and non-mammalian visual systems have led to the hypothesis, as enunciated by such workers as Ramon-y-Cajal (1899) and Le Gros Clarke (1962,1970), that the mammalian visual system evolved to gain the capacity for stereopsis.

This has been termed the elite hypothesis by Fox (1978) as it restricts stereopsis to a small number of frontally eyed more recently evolved mammals. In examination of non-mammalian species Fox (1981) reports that they reveal:

> many special adaptations for binocularity such as a second fovea in the temoral retina, convergence eye movements, and such specializations as sighting grooves - a paring away of the snout so that eyes can look at a common segment of visual space.... (p.359)

Thus Fox (1978) proposes a 'proletarian hypothesis' which holds that all animals that have the capacity for binocular vision also possess stereopsis.

1.5.8.1 *Reptiles and Insects*

Stereopsis has been reported to be present in both the toad (Collett, 1977) and the praying mantis (Rossel, 1983). Both species have large binocular fields and relatively immobile eyes. By placing prisms before their eyes, the convergence angle was altered thus displacing the image of the target (mealworms or a vibrating fly). Under these conditions, both species were shown to have a systematic localization error when they attacked their prey. All strikes were released when the approaching target arrived within a small range of convergence angles, regardless of prism strength.

In these studies the convergence angle was defined as equal to retinal disparity with geometrical respect to the forward looking foveas, that is, a hypothetical point at infinity. As mantids are unable to spontaneously alter the angle of convergence and as the eyes of the toad 'are almost locked in their sockets' (Collett, 1977), both animals have in one sense a fixed horopter. It would seem likely therefore that the transition from a double to a single image is a

salient and sufficient cue to strike. Since only one target was used in these studies, both Collett and Rossel were measuring absolute egocentic distance localization, not relative depth perception and the latter has never been considered a prerequisite for the former.

Evidence for the use of two eyes in estimating egocentric distance in insects was first described in detail by Baldus (1926; cited in Shinkman, 1962). He found that dragonflies rendered monocular responded almost regardless of distance, to stimuli subtending the same visual angle as that subtended by normal prey within reach. It has also been known that one-eyed dragonfly larvae, tiger beetles, praying mantids and water scorpions rarely catch prey (Maldonado & Levin, 1967; Maldonado & Barross-Pita, 1970). It is indeed unfortunate that the process of using convergence for the estimation of egocentric absolute distance has been referred to as stereopsis as it is not analagous to the conventional use of the term in describing a stereoscopic depth mechanism. The confusion may have arisen by the use of the term 'stereopsis by triangulation' by Linksz (1952) to indicate absolute estimation of distance in terms of convergence angle.

Collett (1977) also showed that toads estimate the distance of prey almost as well with one eye as with two. As Ingle (1968) originally proposed, they do this by monitoring the accommodative state of their eyes when the prey is in optimum focus. Such a process was suggested by Fovel in 1910 (cited in Shinkman, 1962). Ingle (1972) also concluded that "no evidence was obtained to support the idea that frogs share a capacity for 'stereoscopic perception' with the higher mammals".

1.5.8.2 *Birds*

Stereopsis has been demonstrated behaviourally in the American kestral (Fox, Lehmkuhle & Bush, 1977) a predatory raptor with extensive binocular overlap provided by well developed temporal foveas and keen vision. Dynamic RDS were used with red and green filters placed before the eyes and the bird was rewarded for flying to a display containing the stereoscopic form. Control conditions included testing performance under monocular conditions and presentation of very large disparities that prevented clear perception of the stereoscopic form. As the bird would not fly with one eye covered, each eye was covered with filters of the same colour thus making only one dot matrix visible. The failure to discriminate under these control conditions indicated that the discrimination was based upon stereopsis. To test for the sensitivity of the bird to configuration, they rotated the stereoscoic form by 90°. Under this condition the discrimination had to be relearnt, suggesting that the falcon was not simply responding to 'something' in depth but considered the stimulus as a function of at least two variables.

When disparity was varied in discrete steps (a difficult session interspersed with an easy discrimination), performance was maximal between 8-12 min of arc and fell below chance for a disparity of 2 min of arc.

1.9 EVOLUTION OF BINOCULAR VISION

The behavioural evidence indicates that in addition to a range of mammals, some birds also possess stereopsis. Indeed both the owl (Pettigrew & Konishi, 1976) and the kestral (Pettigrew, 1979) have neurones tuned to binocular disparity in the visual Wulst. Hence, to

date, stereopsis has only been shown to be present in frontally eyed species that have a predatory life style.

Frontal eyes refers to a small divergence of the optic axes, the absence of a panoramic field to the rear of the head and a wide binocular field. For many writers the implicitly associated wide binocular field simply: "provides an essential basis for stereoscopic vision" (Le Gros Clarke, 1962) and the frontal condition requires no further explanation.

Johnson (1901) concluded that the width of the binocular field is determined by the phylogenetic status of the species: "the higher the order, the nearer the axes approach parallel vision". Implicit in this statement is the belief in the *Scala naturae* (Hodos & Campbell, 1969). Furthermore, such a correlation was challenged by Harris (1904) who contended that the presence of binocular vision was dependent on a particular species' feeding habits. Hence, laterally placed eyes are found in the herbivores and rodents, while perfect binocular vision is found in the carnivores and primates. He correlated such a division with hunted versus predator affinity.

It is often true that within one class predators possess wider binocular fields than their prey. However, cross-class comparison yields such puzzles as to why the width of the binocular field in the predatory crocodile is as narrow (25°) as that of the rabbit and smaller than in the ungulates (Hughes, 1977). A further difficulty with Harris' theory is that primates are not necessarily predators. Harris was content to accept this apparent anomaly as related to the interconnected development of sight and the use of the hand as a prehensile organ.

Eye-hand coordination was again taken up by Elliot-Smith (1928, 1930) and his school (Wood Jones, 1926; Le Gros Clarke, 1962, 1970; Hill, 1972). His arboreal theory (Howells, 1947) is that the frontal--eyed, prehensile, extant primates have evolved from non-prehensile lateral-eyed precursors under the influence of selection pressures arising in arboreal locomotion *per se*. Nevertheless, Haines (1958) has pointed out that although the primates show structural specialization for the arboreal habitat, there are few such gross changes amongst the arboreal carnivores.

According to Duke-Elder (1958), the wide binocular field simply provides stereopsis over a more extensive range of visual space, the value of which aids in:

> pursuit and attack by the predator, in its ordinary activities by the arboreal animal, or by the primate, the eyes of which have become accurately correlated with the use of its hands

Walls (1942) saw stereopsis to be of some use to all species, so that there is a "universal urge to binocularity". However, frontal vision occurs at the expense of the panoramic field, and Walls believes that the width of the binocular field follows passively and inversely upon a particular species' need for panoramic vision.

It remains true that the limitations on the extent of the uniocular optic field ensure that only a small binocular field is possible in lateral eyed species. Defencelessness or lack of cover in their environment (Walls, 1942) requires an almost complete panoramic field of view which will allow detection of enemies coming in any direction without recourse to head or eye movement. Indeed, one can also argue that the disappearance of the rear panoramic field in frontal eyed species is much less significant when the movement of the

eyes and head are taken into account. The 72° blind area to the rear of the head in man is totally eliminated if the head is permitted to rotate.

Common usage equating frontality with binocular vision fails to separate binocular field width from that of stereoscopic vision quality. Hence you will find it said that binocular vision is poorest in lateral eyed species which also probably lack stereopsis (Elliot-Smith, 1930; Cartmill, 1974). Contrary to this view, Hughes (1977) argues that binocular vision is at least universal among mammals, and stereoscopy not justifiably regarded as absent from any mammal possessing a binocular field. Taking this view further, the proletarian hypothesis espoused by Fox (1978, 1981) implies that stereopsis is not an emergent capacity bestowed on a relatively small number of elite animals, but may be a fundamental attribute of vertebrate vision.

CHAPTER TWO

DEMONSTRATION OF BINOCULAR DEPTH PERCEPTION IN THE PIGEON

CONTENTS

2.1 INTRODUCTION

The accurate perception of the relative position of objects in depth is clearly necessary for fine spatial localization. It is well known that the visual system of man is equipped to deal with both monocular (relative size, interposition, linear and aerial perspectives, motion parallax, light and shade and accommodation) and binocular (convergence and stereopsis) cues to depth. The most compelling cue is that of stereopsis, which is a function of binocular vision in which the horizontal disparity between the two retinal images is correlated. This allows dynamic measurement of the relative distances of objects in visual space and is accompanied by the perception of solidity.

Stereopsis was said to have been dependent upon three factors: frontally placed eyes to allow considerable overlap of the binocular visual fields; coordination of eye movements to allow stimulation of corresponding retinal points; and semi decussation of the optic tract to permit interaction of the corresponding images (see Bishop, 1981). The mammalian visual system features such qualities and stereopsis has been demonstrated behaviourally in the monkey (Bough, 1970) and cat (Fox and Blake, 1971).

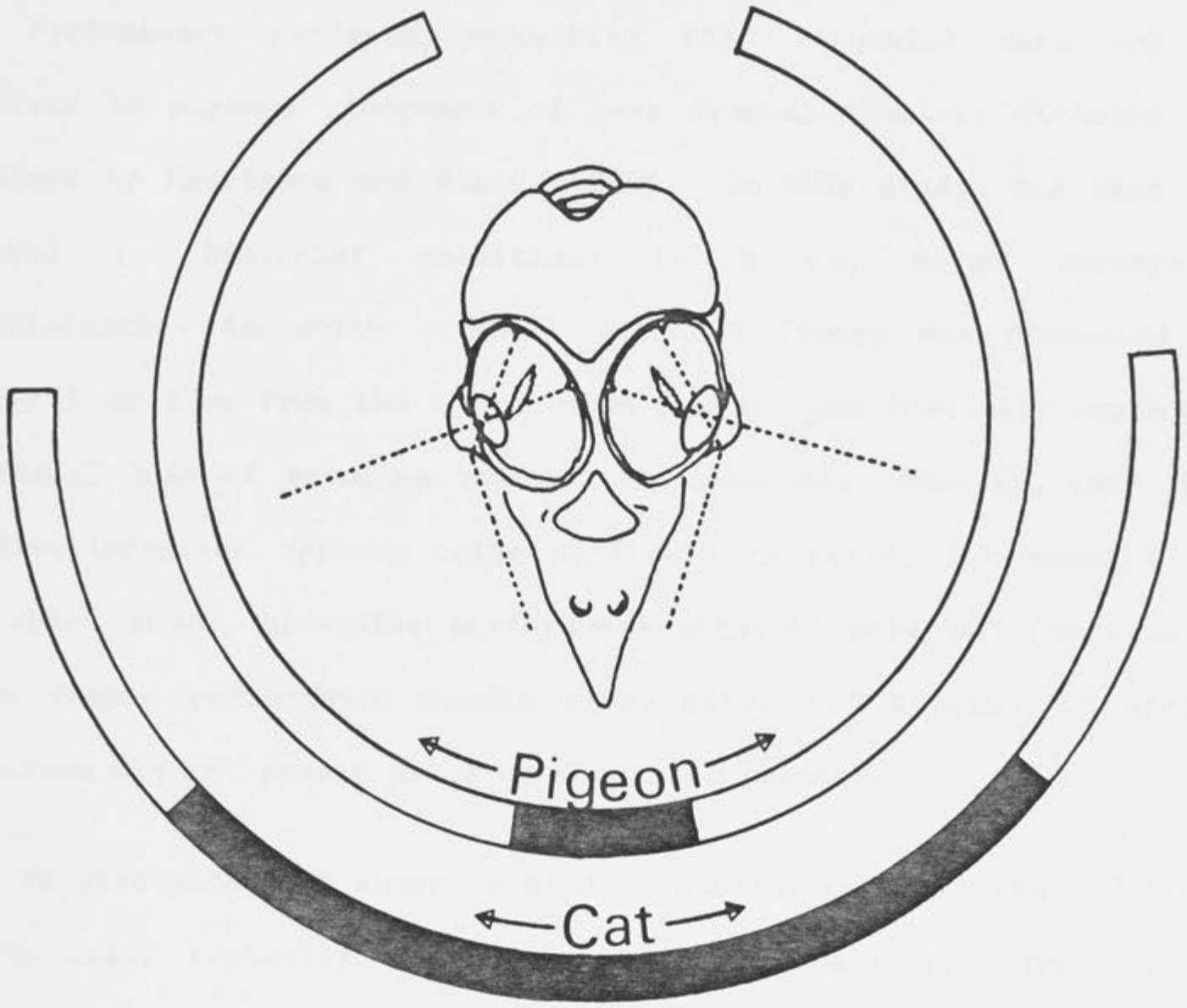
In contrast to mammals, birds have complete decussation at the optic chiasm, yet neurones sensitive to binocular disparity have been found in the owl (Pettigrew and Konishi, 1976a) and kestrel (Pettigrew, 1979) and stereopsis has been demonstrated behaviourally in the latter (Fox *et al.*, 1977). Information from each eye must then be correlated via a partial decussation at some stage in the visual pathway after the optic chiasm.

The frontally eyed owl and the bifoveate kestrel are both raptors with relatively large binocular fields. Despite the fact that there are no vertebrates which are known to have no binocular field, binocular overlap is only regarded as functional stereoscopically in a handful of animals. In particular, stereopsis has long since been regarded as a result of the need for precise spatial localization in animals which hunt and catch prey. Walls (1942) says on this matter:

> The hunters tend towards frontality so as to have the best vision of the prey they are pursuing, while the hunted tend to retain laterality of eye position so as to be able to detect an enemy coming from any direction (p. 290).

The pigeon is primarily a granivorous bird which does not hunt prey and retains the advantages of panoramic vision (approximately 180° according to Chard and Gundlach, 1938) with laterally placed eyes. The optic axes of the pigeons' visual system form an angle of 145° (Donovan, 1978) and allow approximately 24° of binocular overlap (Chard and Gundlach, 1938; Galifret, 1968; Martinoya *et al.*, 1981; Martin and Young, 1983). The lateral position of the eyes are depicted in Figure 2.1 which shows for comparison the extent of the binocular field of the frontally directed field of the cat. Convergence eye movements, elicited mostly by stimuli suddenly appearing in the binocular field (Bloch *et al.*, 1981) would extend the small binocular field. The binocular field also coincides with the area in which localization of food relative to the beak occurs (see section 4.5).

The successful employment of monocular cues to depth in this frontal visual field relies to a greater extent on learning (Hochberg, 1964) and lacks the advantages of the automatic qualities of binocular stereopsis and/or convergence. Indeed if Hess (1956) is correct in saying that the visual apparatus for pecking at grain in young chicks



Region of Binocular Overlap

Figure 2.1 Schematic diagram of the position and relative size of the panoramic visual field of the pigeon and the region of binocular overlap (dark shaded region). Dotted lines represent the projection to the fovea from the lateral fields (optic axes) and the specialized 'red-area' in the temporal retina that receives input from the binocular visual field. The frontal field of the cat is shown for comparison.

is innate and not learned, it would seem likely that the accurate spatial localization seen in pecking for grain in the pigeon (Zeigler, 1980), occurs through the particular use of the binocular quality of the frontal field.

Preliminary evidence suggesting that binocular cues may be involved in pigeons' judgement of near frontal *absolute distance* was obtained by Martinoya and Bloch (1980). In this study, one bird was trained in binocular conditions in a go, no-go successive discrimination in which a small stimulus (lamp) was presented at either 5 or 13cm from the eyes. When one eye was frontally occluded, a gradual loss of stimulus control was observed. However, this type of discrimination appears quite difficult to learn, for example, in the above study, binocular performance attained only 60% (on a scale where chance performance equals zero) after 600 trials. A strict criterion was not passed prior to monocular testing.

We also attempted numerous studies similar to Martinoya and Bloch (1980) using frontally restricted viewing conditions. Two targets (white discs) were presented so that they varied in *relative distance* or depth for different absolute distances from the pigeon (McFadden and Wild, unpublished observations). Whether a Lashley jumping stand modified for birds, or an operant key-pecking situation was used, performance acquisition was painfully slow. Stimulus control increased the closer the stimuli were to the subject, but was inadequate for the measurement of depth thresholds. Replacing the two targets with a single target, it was found the pigeons could successively discriminate a difference in absolute distance of less than 3cm, provided the target was close to the subject (5cm).

The above studies used objects displaced in real space. They indicate that for frontal viewing, stimulus control was best if the

stimuli were close to the subject. Indeed, it has been found, in agreement with Catania's (1964) suggestion of a relatively myopic frontal field, that visual acuity in the frontal field decreases with distance (Bloch and Martinoya, 1982). In order to ascertain whether the pigeon uses a binocular mechanism for depth localization, whether by the use of stereopsis and/or convergence, I chose to use stimuli under free viewing conditions, but which by their intrinsic qualities, could be maximally discriminated through the utilization of binocular cues to depth. These stimuli could be positioned directly behind the keys in a simultaneous operant conditioning paradigm. As pecking the keys was the desired operant response, the stimuli were thus close to the bird and presumably within their accommodative range.

The stimuli were based on a clinical test of stereoacuity in young children devised by Frisby (cited by Hinchliffe, 1978). Apart from its simplicity and versatility, this test has the distinct advantage over haploscopic devices, including random dot stereograms, in that red/green or polarized goggle systems are not used. The difficulty of using these latter devices with animals arises from the impossibility of perfectly matching *perceived* colour achieved via a filter with the spectral sensitivity of the bird. The dichoptic polarization system is also apt to produce luminance changes as a function of head-tilt (Cowey *et al.*, 1975). In addition, unlike haploscopic devices, the Frisby real depth targets maximally stimulate the binocular system. Thus, not only retinal disparity, but also convergence can be theoretically utilized to aid the discrimination.

The aim of this present chapter was to discover whether the pigeon could discriminate depth from non-depth using the Frisby stimuli. Due to the nature of the stimuli, fast acquisition of such a discrimination would be evidence in itself, that binocular cues are

used for the perception of depth. If such a notion is true, it would also be expected that monocular performance on the Frisby discrimination should be inferior to discrimination under normal binocular conditions.

2.2 METHODS

2.2.1 Subjects and Design

A total of 36 experimentally naive feral pigeons (*Columba livia*) were used. Birds were caught locally and held in an outdoor aviary until they were caged for the period of experimental testing. This period varied from 2 months to 2 years. The cages measured 50x50x50 cm and were housed in a constant temperature (25°C) room on a 12 hour light/dark cycle. Directly after caging, pigeons were maintained on an *ad-libitum* diet of mixed pigeon grain and water for 7-10 days. At the end of this period, each bird was weighed daily for 6-8 days in order to establish the mean 100% free-feeding body weight. The mean 100% body weight for all birds was 353gms (σ_{n-1} = 50gms). Birds were then slowly reduced to 80% of their free-feeding weight over a period of 2-3 weeks. All birds were then continuously maintained at 80% of their free-feeding weight during the entire experimental session. *Ad-libitum* water was always available in the home cage.

The subjects were divided into the groups shown in Table 2.1. Group 2 represents a compilation of subjects used in this and in experiments reported in subsequent chapters.

Group No	Group Description	Subject Identification Numbers
1	SDT	15 16 18 20
2	SDT Compiled	8 9 10 11 18
		20 31 32 33 35
		36 37 38 39 40
		45 46 47 48 49
		50 51 52 53 55
		34 54 66
3	Monocular/SDT	8 9 10 11
		37 40 50
4	Monocular/Pattern 1	17 19 24
5	Monocular/LDT	12 13 14
6	RDT	35 37 39 40

Table 2.1 Assignment of subjects to groups: SDT, Standard Depth Task; LDT, Less Dense Task; RDT, Relative Depth Task. See text for further explanation.

2.2.2 Apparatus

Subjects were trained in one of three two-key operant chambers (type BRS/LVE). Two clear perspex keys (47 x 47mm) horizontally separated by 15mm, were mounted 170mm above the floor. The access to the grain hopper was located 40mm above the cage floor midway between the response keys. A motor-driven bracket mounted on a moveable plate enabled one of two stimuli to be simultaneously positioned directly

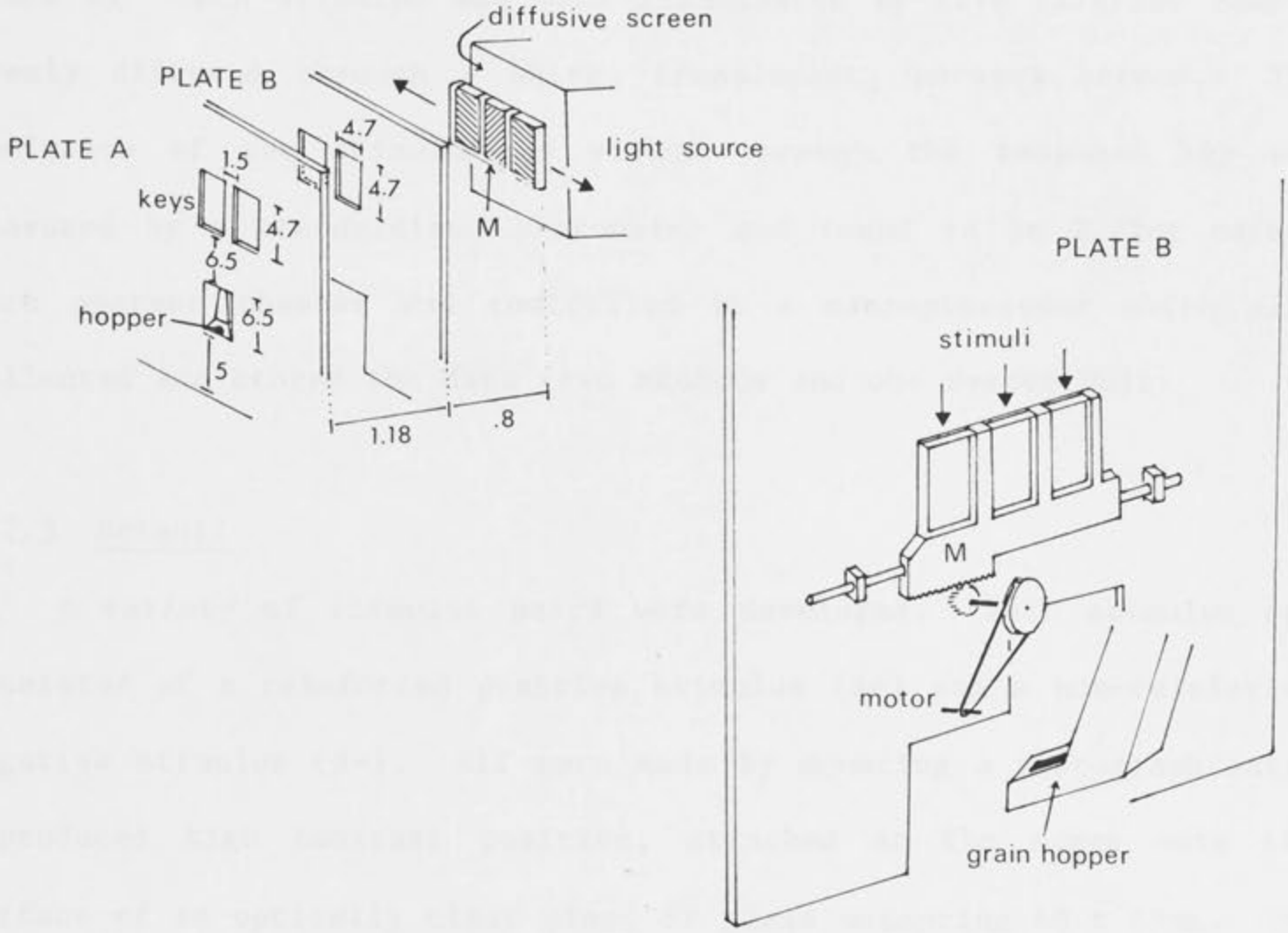


Figure 2.2 Exploded view of apparatus (not to scale). Distances in cm. Plate A was fixed, plate B, the back of which is shown in detail, was able to be moved at variable distances behind plate A. Except during threshold testing, this distance was set at 1.2 cm. The stimuli were inserted into the motor driven bracket (M) which could be moved to enable one stimulus to be visible behind each key.

behind either response key. The distance from the response key to the front of the stimulus was 19.9mm (Figure 2.2). Masking noise was produced by a fan placed in the back left hand corner of the chamber. The interior of the chamber was illuminated by a 45w lamp mounted in the centre of the ceiling. The ceiling was located 21 cm above the top of the response keys, and the lamp was 30 cm in front of plate A. Each stimulus was back illuminated by five .17A/28V lamps, evenly diffused through a white, translucent, perspex screen. The luminance of the stimulus as viewed through the response key was measured by a standardized photometer and found to be 2.7log cd/m^2. Each operant chamber was controlled by a microprocessor which also collected and stored the data (two MR6800s and one System 80).

2.2.3 Stimuli

A variety of stimulus pairs were developed. Each stimulus set consisted of a reinforced positive stimulus (S+) and a non-reinforced negative stimulus (S-). All were made by mounting a photographically reproduced high contrast positive, attached at the edges onto the surface of an optically clear piece of glass measuring 48 x 65mm. The thickness of the glass depended upon the type of stimulus and is defined below. Each stimulus was viewed through a 47 x 47mm aperture thus masking the edges of the stimulus.

2.2.3.1. *Standard depth task (SDT)*

The standard depth task (SDT) consisted of a stimulus pair where S+ = D10 and S- = CD10.

CD10: The control depth 10 stimulus consisted of an array of random sized triangles placed onto the front side of a piece of optically clear glass 10mm thick (Figure 2.3a).

D10: The depth 10 stimulus consisted of an identical array to CD10 divided into two components such that a centre circular portion of the array (containing only whole triangles) was displaced onto

the back of a piece of optically clear glass 10mm thick. The remaining surround was on the front of the same piece of glass (Figure 2.3b). Hence the image present was of a circle displaced 10mm in depth from the surround. When viewed monocularly from a direct stationary position, the circle was no longer visible and D10 appeared equivalent to CD10.

2.2.3.2. *Less Dense Task (LDT)*

The less dense task (LDT) consisted of a stimulus pair where S+ = LD10 and S- = CLD10.

CLD10: The control less dense depth 10 stimulus was identical to CD10 except the *density* of the random sized triangle array was reduced by a factor of two (Figure 2.3c).

LD10: The less dense depth 10 stimulus was identical to D10 except that the two components were based on the reduced density array of CLD10 (Figure 2.3d).

2.2.3.3. *Relative Depth Task (RDT)*

The stimulus set for the relative depth task (RDT) consisted of S+ = D10 and S- = D10 inverted.

D10 inverted : identical to D10 except that the surround portion of the array was displaced onto the *back* of the glass leaving the centre circular array on the front of the glass.

2.2.3.4. *Pattern 1*

The stimulus set for pattern 1 consisted of S+ = P1 and S- = CP1. An identical array to that of CD10 was divided into a centre circular portion and the remaining surround. The centre circle was made large enough so that the total area and the number of triangles in each component were equal.

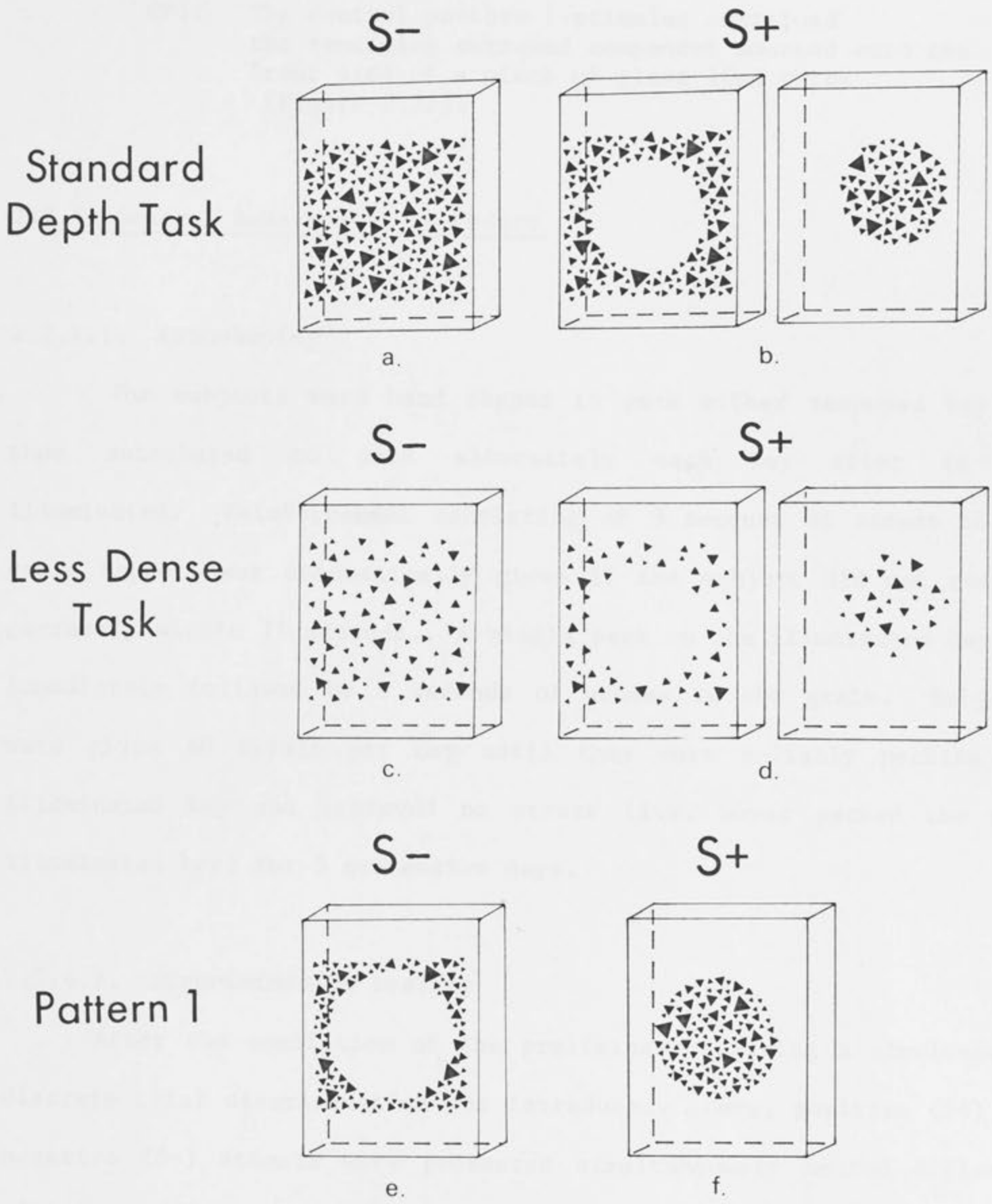


Figure 2.3 Stimulus configurations for the standard depth task (a,b), less dense task (c,d) and pattern 1 task (e,f): a,c and e represent the negative stimuli (S-); b,d and f represent the positive stimuli (S+). The two parts to b and d are separated to show the front and back faces of a single stimulus.

P1: The pattern 1 stimulus contained the centre circular component mounted onto the front side of a piece of glass 10mm thick.

CP1: The control pattern 1 stimulus contained the remaining surround component mounted onto the front side of a piece of glass 10mm thick (Figure 2.3f).

2.2.4 General Behavioural Procedure

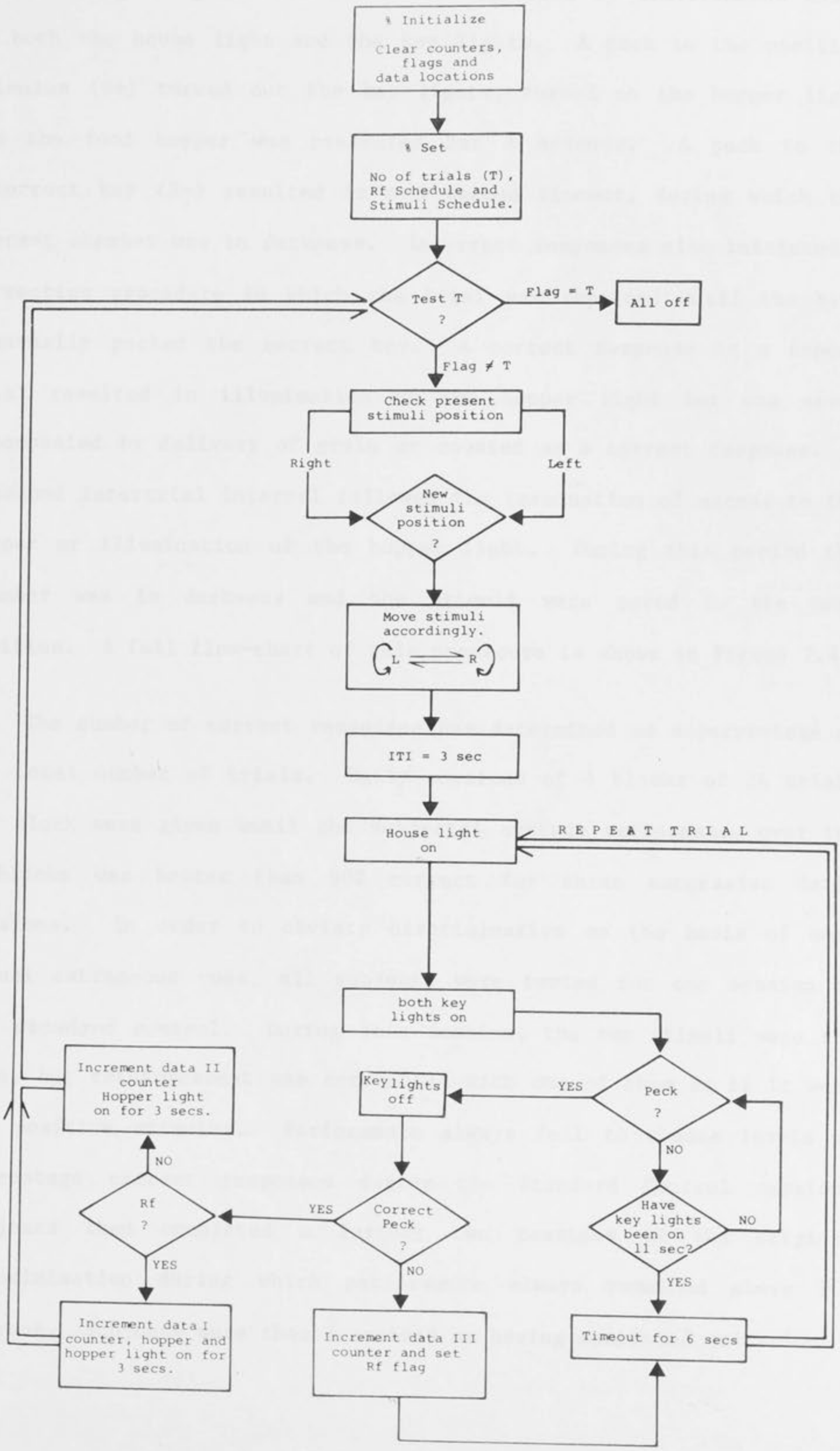
2.2.4.1. *Autoshaping*

The subjects were hand shaped to peck either response key and then autoshaped to peck alternately each key after it was illuminated. Reinforcement consisting of 3 seconds of access to the grain hopper, was automatically given if the subject did not respond correctly within 11 seconds. A single peck on the illuminated key was immediately followed by 3 seconds of access to the grain. Subjects were given 60 trials per day until they were reliably pecking the illuminated key and achieved no errors (i.e. never pecked the non-illuminated key) for 3 successive days.

2.2.4.2. *Discrimination testing*

After the completion of the preliminary training a simultaneous discrete trial discrimination was introduced. Here, positive (S+) and negative (S-) stimuli were presented simultaneously behind different illuminated keys, and were switched between trials according to a computer generated quasi-random sequence. The stimuli were always made to move the same distance between trials even when the move resulted in the stimuli resuming their original positions. This was done to obviate discrimination on the basis of noise produced by movement of the stimuli.

Figure 2.4 Flow chart of the behavioural discrimination based upon a simultaneous discrete trial operant procedure. During Timeout the chamber was in complete darkness. Rf, Reinforcement; ITI, intertrial interval.


% Initialize
Clear counters, flags and data locations
% Set
No of trials (T), Rf Schedule and Stimuli Schedule.
Test T ?
Flag = T
All off
Flag ≠ T
Check present stimuli position
Right
Left
New stimuli position ?
Move stimuli accordingly.
L
R
ITI = 3 sec
House light on
REPEAT TRIAL
both key lights on
Peck ?
YES
Key lights off
NO
Have key lights been on 11 sec?
NO
YES
Timeout for 6 secs
Correct Peck ?
YES
NO
Rf ?
NO
YES
Increment data II counter Hopper light on for 3 secs.
Increment data I counter, hopper and hopper light on for 3 secs.
Increment data III counter and set Rf flag

The beginning of each trial was signalled by simultaneous onset of both the house light and the key lights. A peck to the positive stimulus (S+) turned out the key lights, turned on the hopper light and the food hopper was presented for 3 seconds. A peck to the incorrect key (S-) resulted in a 3 second timeout, during which the operant chamber was in darkness. Incorrect responses also initiated a correction procedure in which the trial was repeated until the bird eventually pecked the correct key. A correct response in a repeat trial resulted in illumination of the hopper light but was never accompanied by delivery of grain or counted as a correct response. A 3 second intertrial interval followed the termination of access to the hopper or illumination of the hopper light. During this period the chamber was in darkness and the stimuli were moved to the next position. A full flow-chart of this procedure is shown in Figure 2.4.

The number of correct responses was determined as a percentage of the total number of trials. Daily sessions of 4 blocks of 24 trials per block were given until the subjects' average performance over the 4 blocks was better than 90% correct for three successive daily sessions. In order to obviate discrimination on the basis of non-visual extraneous cues, all subjects were tested for one session on the *standard control*. During this session, the two stimuli were the same, but reinforcement was correlated with one of them as if it were the positive stimulus. Performance always fell to chance levels of percentage correct responses during the Standard Control session. Subjects then completed a further two sessions of the original discrimination during which performance always remained above 90% correct. Subjects were then described as having completed criterion.

2.2.4.3. *Monocular testing*

Subjects from experiments described in Chapters 2 and 5 were tested on various discrimination tasks with one eye covered. Occlusion was achieved by the application of a small light-tight, felt-lined rubber goggle that neatly fitted over either eye without contacting the eye or lid. The goggle was attached by the use of velcro tape (Figure 2.5). A ring of the hooked side of the tape was glued onto the feathers around each eye with a mild contact adhesive (Plate 2.1) and allowed to dry overnight. The other side of the velcro tape was fitted around the base of the goggle. The goggle could then be attached to either velcro ring (Plate 2.2) simply by contact of the velcro tape. Once attached, it could be removed by holding the base ring firmly and gently peeling the velcro apart.

Occlusion of the eye in this fashion had a number of advantages. Firstly, the goggle was light and appeared comfortable as evidenced by the bird's rapid adaptation to its presence. Secondly, it was secure and could not be removed by the subject. Finally, the method allowed easy transfer of the goggle from one eye to the other.

2.2.5 Behavioural Procedure for Individual Groups

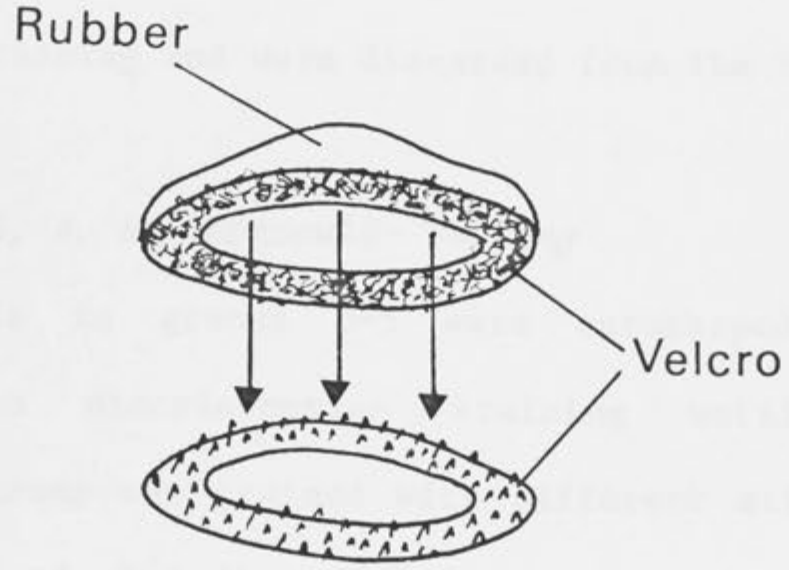
2.2.5.1 *Group 1 - Standard Depth Task (SDT)*

All subjects were autoshaped and transferred immediately onto discrimination training as already described. The stimuli were those constituting the SDT. Two subjects were randomly selected (18 and 20) and trained with S+ equivalent to D10 and S- equivalent to CD10. The remaining two subjects (15 and 16) were trained with the opposite stimulus conditions. Hence the positive and negative stimulus conditions were counterbalanced. Following the completion of criterion all subjects were given one session in which the triangle

Plate 2.1 Position of the velcro ring to which the goggle was attached during monocular occlusion.

Figure 2.5 Attachment of goggle to velcro ring.

Plate 2.2 Goggle in position during monocular occlusion.


Rubber
Velcro

arrays were mounted onto a frame of balsa wood instead of the optically clear glass. The balsa wood stimuli appeared identical to those used in the SDT (the balsa wood edges being masked) except that free space replaced the glass medium. This control was simply to ensure that no luminance cues due to any aspect of the optically clear glass were present.

2.2.5.2 *Group 2 - SDT, Compiled.*

A further 28 subjects were subsequently trained on the SDT in an identical fashion to subjects 18 and 20 above. Three of the subjects (34, 54 and 56) were unable to perform the discrimination above chance after extended training and were discarded from the data analysis.

2.2.5.3 *Groups 3, 4, 5 - Monocular testing*

Subjects in groups 3-5 were autoshaped and transferred immediately onto discrimination training until criterion was reached. Each group was trained with different stimulus conditions. Group 3 was trained with the stimuli constituting the SDT. Group 4 was trained on the pattern 1 discrimination. This particular pattern was chosen so as to employ the components of the SDT stimuli (equated for area) to serve as S+ and S-. Group 5 was trained on a depth discrimination in which the stimuli (LD10) were a reduced density version of those constituting the SDT.

After the completion of criterion on the appropriate task, all subjects were tested monocularly, as previously described. Two subjects (37 and 40) in group 3 were first tested on the transfer task of group 6 (Relative Depth Task) before monocular sessions were introduced. The delay was 4-6 sessions, after which criterion performance on the SDT was immediately reinstated. After each individual subject completed criterion, velcro rings were glued around

each eye and allowed to dry overnight. In the following session the subject was tested binocularly as before, except with the rings glued in position. Performance during this session always remained above 90% correct. Monocular testing was then implemented where each eye was alternately occluded from session to session. The choice for which eye was occluded for the first session of monocular testing was random. Within one session all subjects were given, in addition to four blocks of monocular trials, one block of binocular trials. Each block consisted of 24 trials. The order of monocular and binocular testing was randomized from session to session. Hence the binocular block was positioned either prior to or after the monocular blocks. Monocular testing was continued for at least the same number of sessions that had been taken by an individual subject to learn the task initially under binocular conditions.

2.2.5.4 *Group 6 - Relative Depth Task*

Four subjects were autoshaped and transferred onto discrimination training with the stimuli that were those constituting the SDT. After completion of criterion, all subjects were tested for transfer to a new stimuli set in which S- was changed to D10 inverted (see Section 2.2.3.3). Both S+ and S- now contained the same components displaced by an equal amount of depth. However, whereas the circle appears behind the surround in S+, the reverse occurs in S-, that is the circle appears in front of the surround.

2.3 RESULTS

2.3.1 Acquisition of the SDT.

2.3.1.1 *Group 1*

All subjects in group 1 were easily able to discriminate between S+ and S-, and learnt the task to criterion irrespective of whether D10 or CD10 served as the positive stimulus. Acquisition curves are shown in Figure 2.6 where the mean percentage correct is plotted as a function of sessions.

A linear regression was fitted to each individual learning curve and it was found that the correlation coefficient, r, was always greater than 0.9. This indicates that the learning curves can be approximated by a linear function, the parameters of which will be used for comparisons between different groups. The slope of the regression line (SL), the number of sessions to criterion (SN) and the correlation coefficients (r) for each subject are shown in Table 2.2.

The mean SL and SN both indicate faster learning by subjects 18 and 20 in which D10 was the positive stimulus. The small number of subjects precludes a statistical evaluation of this result. Nevertheless, all subjects learned the task to criterion. It was also found in this experiment that all subjects maintained criterion levels of discrimination performance (Mean score = 94.8%) when the stimuli were presented on a frame (i.e. with no glass) indicating that the presence of the glass was not providing subtle, unidentified cues to depth.

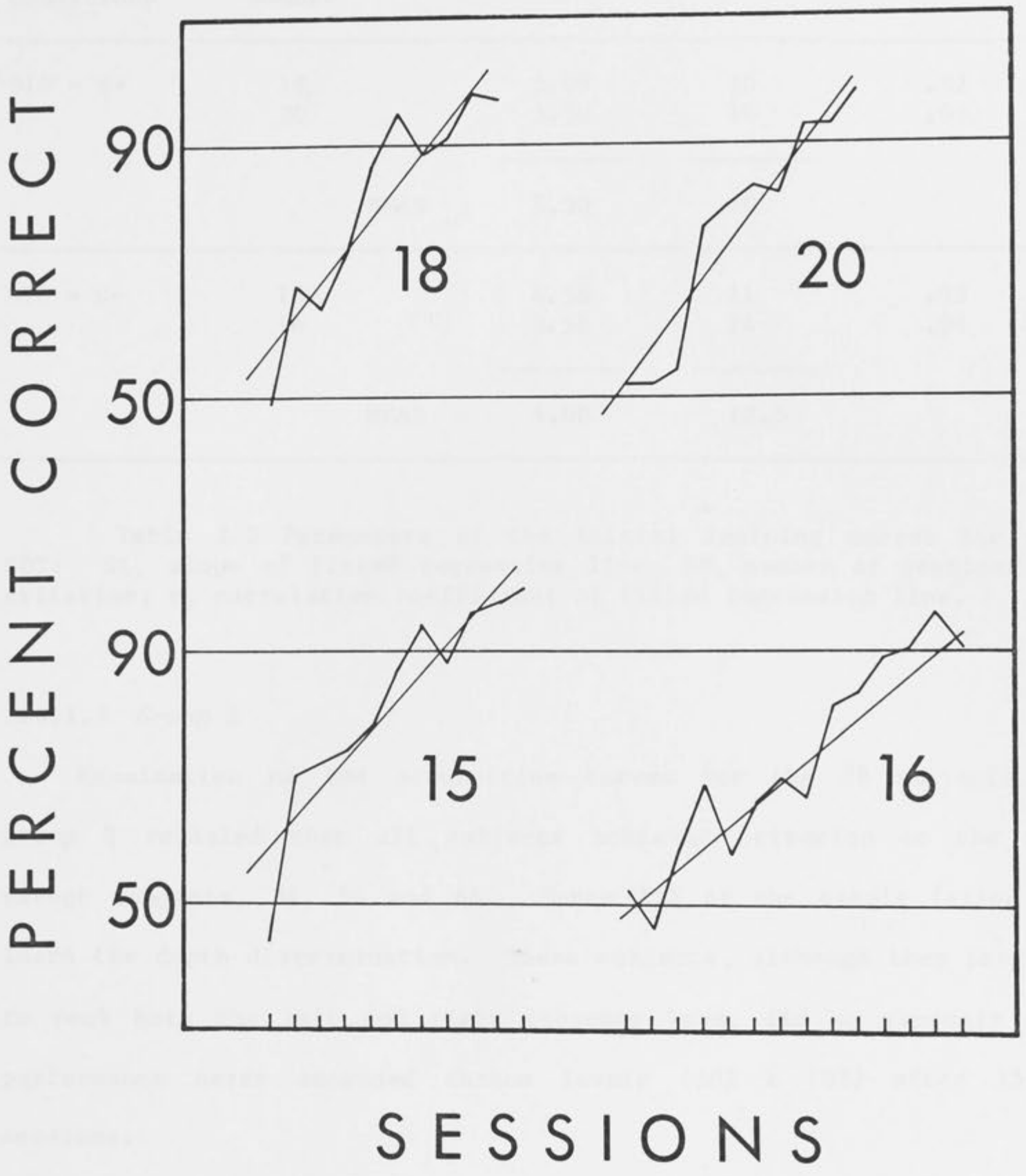


Figure 2.6 Acquisition curves for subjects in group 1 trained on the standard depth task. Subjects 18 and 20 were trained to peck the stimulus with depth present, while subjects 15 and 16 were trained to peck the stimulus without depth. Lines drawn through each curve represent the linear regression fitted to the data. Each pip on the sessions axis is equal to 96 trials (one session).

Stimulus Conditions	Subject Number		SL	SN	r
D10 = S+	18		5.09	10	.92
	20		5.50	10	.95
		MEAN	**5.30**	**10**	
D10 = S-	15		4.58	11	.92
	16		3.58	14	.94
		MEAN	**4.08**	**12.5**	

Table 2.2 Parameters of the initial learning curves for the SDT: SL, slope of fitted regression line; SN, number of sessions to criterion; r, correlation coefficient of fitted regression line.

2.3.1.2 *Group 2*

Examination of the acquisition curves for the 28 subjects in group 2 revealed that all subjects achieved criterion on the SDT except subjects, 34, 54 and 66. Hence 11% of the sample failed to learn the depth discrimination. These subjects, although they learned to peck both the left and right response keys, did so randomly and performance never exceeded chance levels (50% ± 10%) after 15-20 sessions.

The remaining acquisition curves are plotted in Figure 2.7. Each graph shows the development of the mean percentage correct score obtained over sessions. For each subject the SL, r and SN of individual learning curves were calculated and are shown in Table 2.3, according to which month day-one of discrimination training occurred. It should again be noted that SL is a reasonable indication of the rate of learning for a particular subject as r in general indicates a good linear relationship between SN and the mean

Figure 2.7 Acquisition curves of the standard depth task for all subjects in group 2. Subject identification numbers are indicated on the right side of each individual learning curve. Points lying near the 50% correct line represent chance performance. Three consecutive points above the 90% correct line constitute criterion. Each point represents one session.

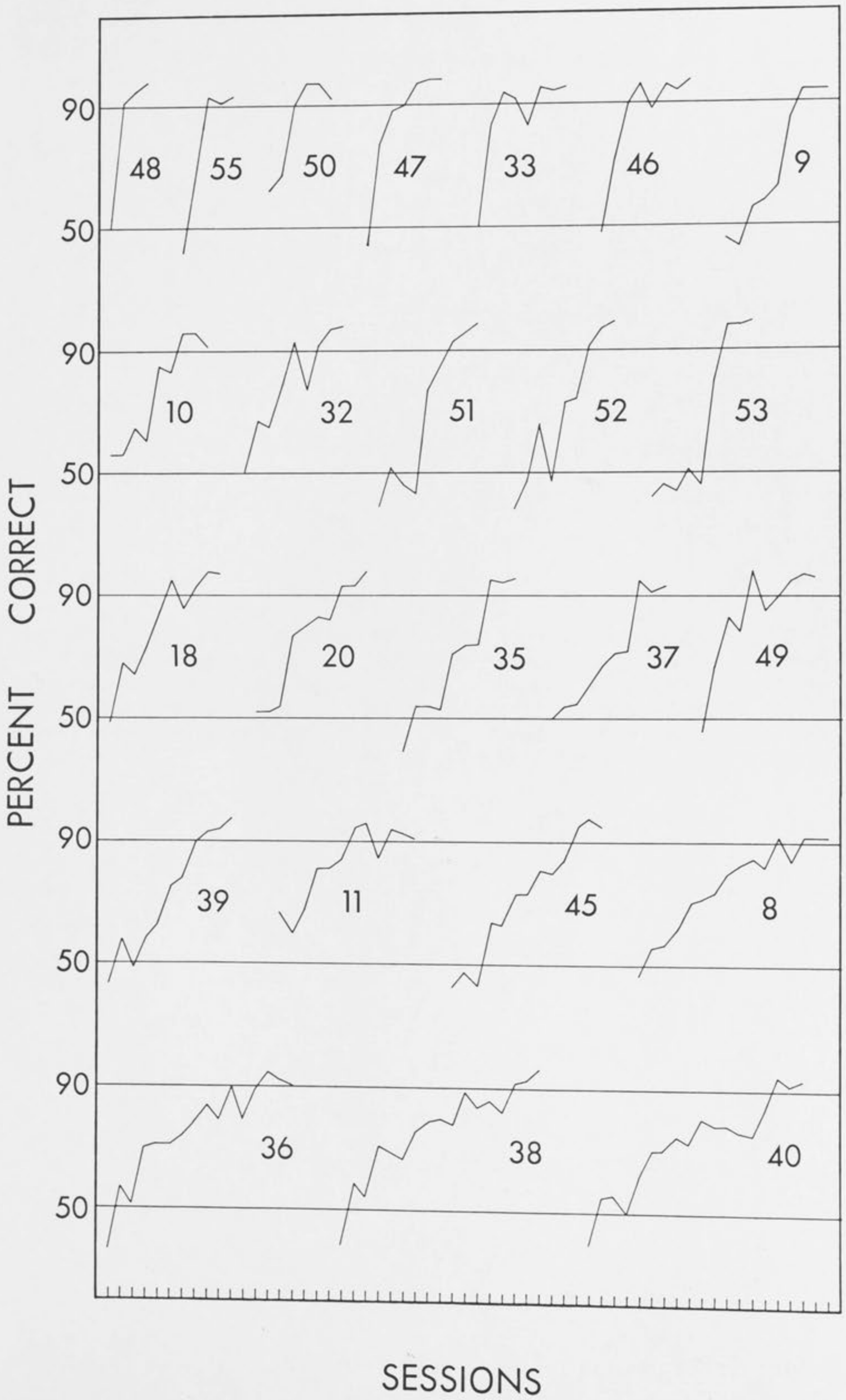

PERCENT CORRECT
90
50
48
55
50
47
33
46
9
90
50
10
32
51
52
53
90
50
18
20
35
37
49
90
50
39
11
45
8
90
50
36
38
40
SESSIONS

Table 2.3 Parameters of the initial acquisition curves for all subjects in group 2 tabulated according to which month day one of discrimination training began. SL, slope of the linear regression fitted to an individual's learning curve; r, correlation coefficient of the fitted regression line; SN, number of trials taken to reach criterion; S.E., standard error of the mean.

MONTH	SUBJECT	SL(r)	SN	Mean SL S.E.	(Mean r) S.E.	Mean SN S.E.
Jan	8	2.87 (.94)	16			
	9	7.45 (.95)	9	4.81	(.92)	11.75
	10	5.65 (.92)	9	1.07	(.02)	1.70
	11	3.27 (.87)	13			
Feb	45	4.81 (.97)	13			
	46	5.47 (.79)	8			
	48	14.78 (.85)	4	7.52	(.87)	8.33
	49	4.49 (.82)	10	1.58	(.03)	1.28
	50	7.11 (.84)	6			
	51	8.49 (.93)	9			
March	47	7.61 (.84)	7			
	52	7.87 (.94)	9	9.15	(.87)	7.50
	53	8.71 (.91)	9	1.11	(.02)	.96
	55	12.42 (.87)	5			
July	18	5.09 (.92)	10	5.30	(.94)	10.00
	20	5.50 (.95)	10	.29	(.021)	0.00
August	33	4.29 (.69)	8			
	31	3.20 (.95)	18	4.31	(.84)	11.67
	32	5.43 (.87)	9	.64	(.08)	3.18
Sept.	35	6.38 (.96)	40			
	36	3.04 (.90)	16			
	37	5.53 (.92)	10	4.35	(.93)	13.67
	38	2.75 (.92)	17	.70	(.01)	1.52
	39	5.73 (.97)	11	.70	(.01)	1.52
	40	2.67 (.93)	18			
		Grand Mean		**5.9**	**(.90)**	**10.50**

percentage correct obtained for each session. Plots of the mean SL and SN according to month of the year are predicted in Figure 2.8. Here it is immediately apparent that the range of learning rates shown in Figure 2.7 were due to an annual cyclic variation in which learning was poorest during the months of August and September (Southern hemisphere) (see Section 2.4.4).

Thus, except for a small proportion of the population, pigeons can discriminate depth from non-depth in the Frisby stimuli, no matter which serves as the positive stimulus. Furthermore, the discrimination appears to be learnt with ease in an almost linear fashion, requiring a mean number of approximately 1000 trials to reach criterion.

2.3.2 Monocular Performance

The depth stimulus (D10) contains strong binocular cues to depth. The ease with which criterion performance was attained on the standard depth task (SDT) implies that it was likely that subjects utilized these binocular cues in order to make the depth stimulus distinct from the non-depth stimulus. However, the depth stimulus also contains subtle monocular cues, and it is possible that motion parallax, accommodation or monocular cues arising at the edge of the displaced circle may mediate the discrimination. Such monocular cues would still be available with one eye covered. The hypothesis that binocular cues were preferentially used as the basis of the depth discrimination predicts that performance should be severely reduced under monocular conditions. However, if subjects were relying purely on monocular cues, no deficit in performance should be evident after one eye is occluded. This is provided of course, that covering one eye has no non-specific effect on discrimination performance due

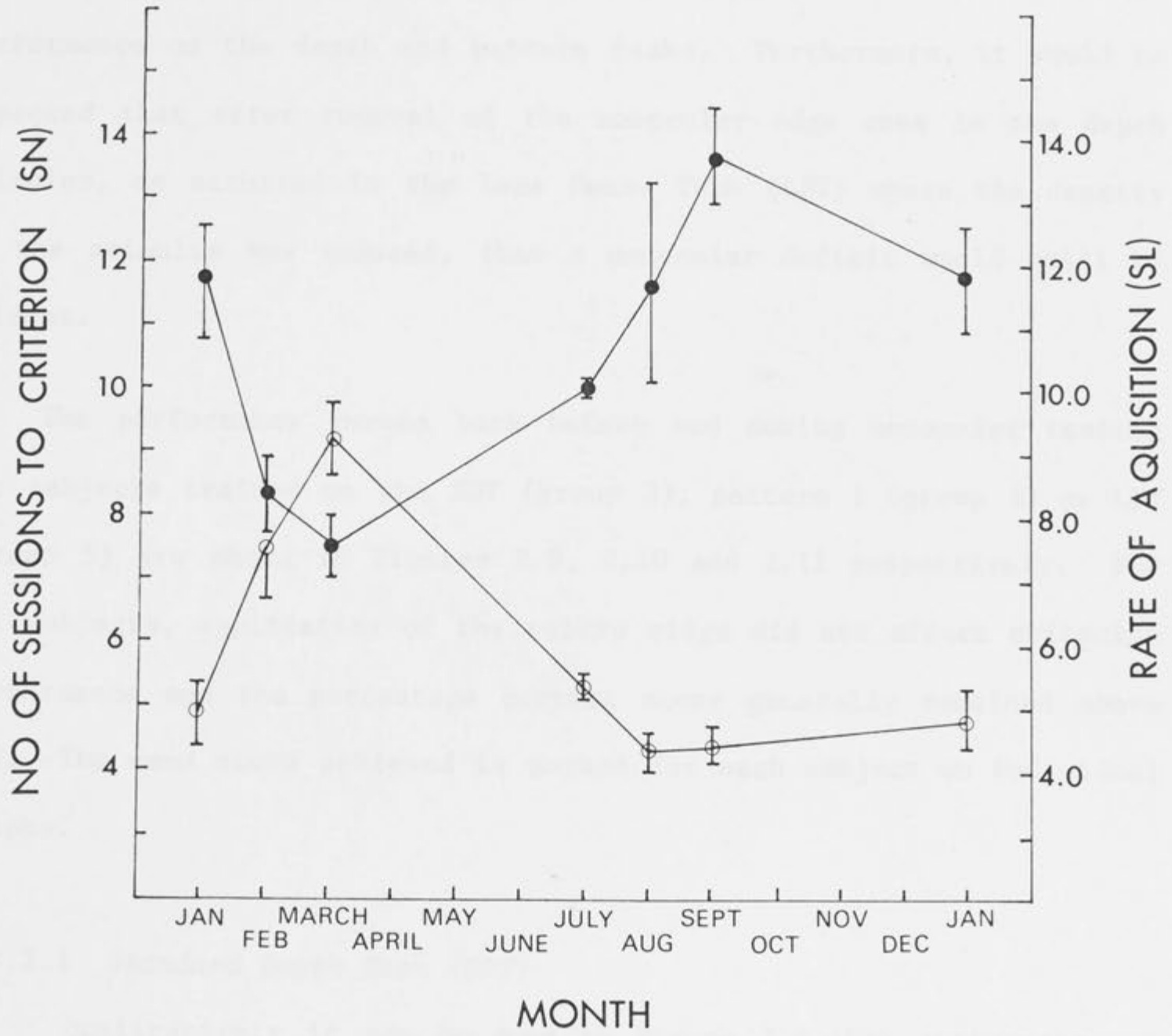


Figure 2.8 The mean number of sessions to criterion (SN, ●) and the mean slope of the fitted linear regression lines (SL, ○) for each subject in group 2 plotted as a function of the month in which day-one of discrimination training on the SDT occurred. Bars on each point indicate the standard error.

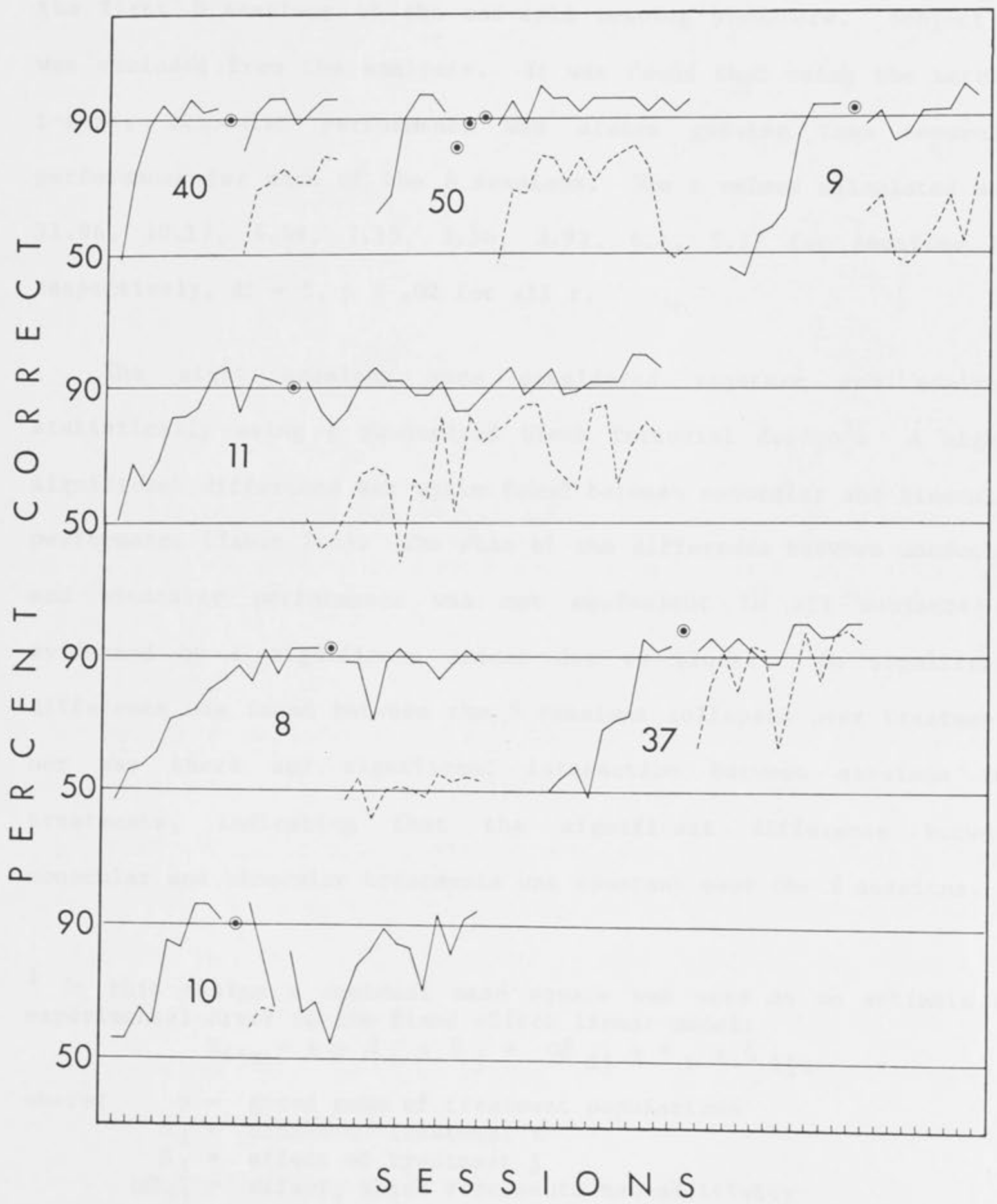
perhaps to blocking half the visual field or wearing the goggle *per se*. Hence, monocular performance of subjects was examined not only on the SDT, but also on a pattern discrimination composed of the components of the D10 stimulus. If binocular cues were used as the basis of the SDT, a differential deficit should be seen in monocular performance on the depth and pattern tasks. Furthermore, it would be expected that after removal of the monocular edge cues in the depth stimulus, as occurred in the Less Dense Task (LDT) where the density of the stimulus was reduced, that a monocular deficit would still be evident.

The performance curves both before and during monocular testing for subjects trained on the SDT (group 3), pattern 1 (group 4) or LDT (group 5) are shown in Figures 2.9, 2.10 and 2.11 respectively. For all subjects, application of the velcro rings did not affect criterion performance and the percentage correct score generally remained above 90%. The mean score achieved is marked for each subject on individual graphs.

2.3.2.1 *Standard Depth Task (SDT)*

Qualitatively it can be seen in Figure 2.9 that performance on the SDT was severely effected by the occlusion of one eye. With training, monocular performance improved for 5 of the 7 subjects to levels better than chance, but except for subject 37, all birds were unable to reach criterion even after extended training (such as the 27 monocular sessions shown for subject 11). Monocular performance was generally highly variable from session to session. In contrast, the single binocular block of trials, although based on a mean of only 24 trials as opposed to 96 trials for the monocular mean, remained relatively constant for all subjects except subject 10. Here, three monocular sessions interfered with binocular performance and resulted

Figure 2.9 The performance curves both before and during monocular testing on the standard depth task (SDT) for subjects in group 3. The numbers beside each graph indicate the subject identification. Each graph shows the initial acquisition curve followed by performance after application of the velcro ring (⊙) and the subsequent binocular performance (———) and concurrent monocular performance (-----). Each point is one session (96 trials).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in extinction of the original discrimination. For this subject the task had to be relearnt binocularly.

Quantitatively, the mean binocular percentage correct score was compared with the corresponding mean monocular score within each of the first 8 sessions of the one-eyed testing procedure. Subject 10 was excluded from the analysis. It was found that using the matched t-test, binocular performance was always greater than monocular performance for each of the 8 sessions. The t values calculated were 11.96, 10.17, 4.49, 7.15, 3.56, 3.92, 6.6, 5.17 for sessions 1-8 respectively, df = 5, $p < .02$ for all t.

The eight sessions were considered together and analysed statistically using a randomized block factorial design[1]. A highly significant difference was again found between monocular and binocular performance (Table 2.4). The size of the difference between monocular and binocular performance was not equivalent in all subjects as evidenced by a significant effect due to blocks. No significant difference was found between the 8 sessions collapsed over treatments nor was there any significant interaction between sessions and treatments, indicating that the significant difference between monocular and binocular treatments was constant over the 8 sessions.

[1] In this design a residual mean square was used as an estimate of experimental error in the fixed effect linear model;

$$X_{ijm} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \pi_m + \xi_{ijm}$$

where; μ = grand mean of treatment populations
α_i = effect of treatment i
β_j = effect of treatment j
$\alpha\beta_{ij}$ = effect, which represents non-additivity of effects α_i and β_j
π_m = a constant associated with block m
ξ_{ijm} = experimental error.

since by application of Tukey's test, $\sum_{i=1}^{p} \alpha\beta_{ij}$ and $\sum_{i=1}^{q} \alpha\beta_{ij}$ are zero ($F = 3.3 \times 10^{-4}$). Hence $\alpha\beta_{ij}$ is equivalent to an effect which represents non-additivity of effects α_i and β_j.

Source	SS	df	MS	F
Blocks	4,431	5	886	12.0**
Treatments	18,919	15	1,261	239.2**
A	17,604	1	17,604	1.9
B	968	7	138	.7
AxB	347	7	50	
Residual	5,517	75	74	
Total	28,867	95		

Table 2.4 ANOVA table for analysis of the standard depth task using a randomized block factorial design. Subjects were treated as blocks and treatments were composed of the difference between monocular and binocular performance (A) and performance over sessions (B). SS, sums of squares; df, degrees of freedom; MS, mean square, **p < .01

It was also of interest to see whether there was any correlation between parameters of the acquisition curves of the SDT and the size of the monocular deficit for each subject (see Section 2.4.1.1). One way to do this is to measure the correlation ratio (r) between either the number of sessions taken to reach criterion (SN) or the slope of the fitted regression line (SL), and the mean difference between binocular and monocular performance scores for the first four or eight sessions of the one-eyed testing procedure. It was found that there was no correlation between SN and the mean difference score for the first four (r = .21) or eight (r = .16) monocular sessions (see scattergram plotted in Figure 2.12). Nor was there any relationship between SL and the mean difference score for the first eight sessions of the one-eyed testing procedure (r = -.17).

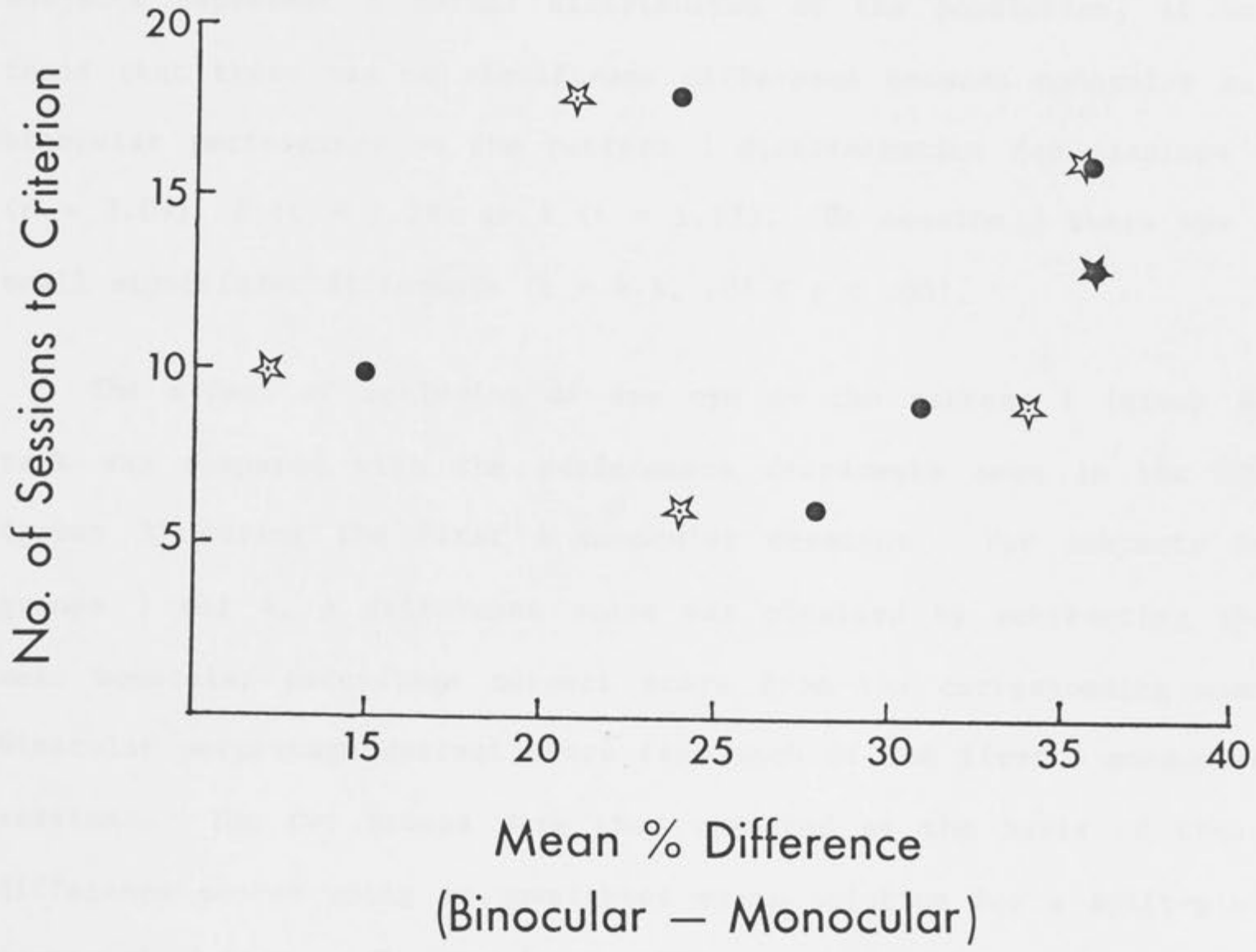


Figure 2.12 Scattergram showing the independence of an individual bird's difficulty in learning the SDT (as measured by the number of sessions taken to reach criterion) and the observed monocular deficit (as measured by the mean difference between binocular and monocular performance) for the first four (●) or eight (☆) sessions of the one-eyed testing procedure.

2.3.2.2 *Pattern 1*

In striking contrast to subjects tested monocularly on the SDT all subjects tested monocularly on the pattern discrimination were generally unaffected by the presence of the goggle (Figure 2.10). Each monocular mean score was compared independently with each binocular mean score for the first 4 sessions of the one-eyed testing procedure using a matched pairs t-test. Assuming that the three subjects represent a normal distribution of the population, it was found that there was no significant difference between monocular and binocular performance on the pattern 1 discrimination for sessions 1 ($t = 2.09$), 2 ($t = 1.74$) or 4 ($t = 1.57$). On session 3 there was a small significant difference ($t = 4.5$, $.01 < p < .05$).

The effect of occlusion of one eye on the pattern 1 (group 4) task was compared with the performance decrements seen in the SDT (group 3) during the first 4 monocular sessions. For subjects in groups 3 and 4, a difference score was obtained by subtracting the mean monocular percentage correct score from the corresponding mean binocular percentage correct score from each of the first 4 monocular sessions. The two groups were then compared on the basis of these difference scores using an unweighted means solution for a split-plot factorial design. The resultant ANOVA table can be seen in Table 2.5. There was a highly significant difference between the pattern and SDT groups, and this difference remained constant over the 4 sessions compared.

It should also be noted that from the initial binocular acquisition curves, the SDT required more sessions on average, and had a slower rate constant than seen for the pattern 1 group (see Table 2.6). The difference in the number of sessions taken to learn the two tasks initially, was significant ($t = 2.46$, $p < .025$, $df = 7$).

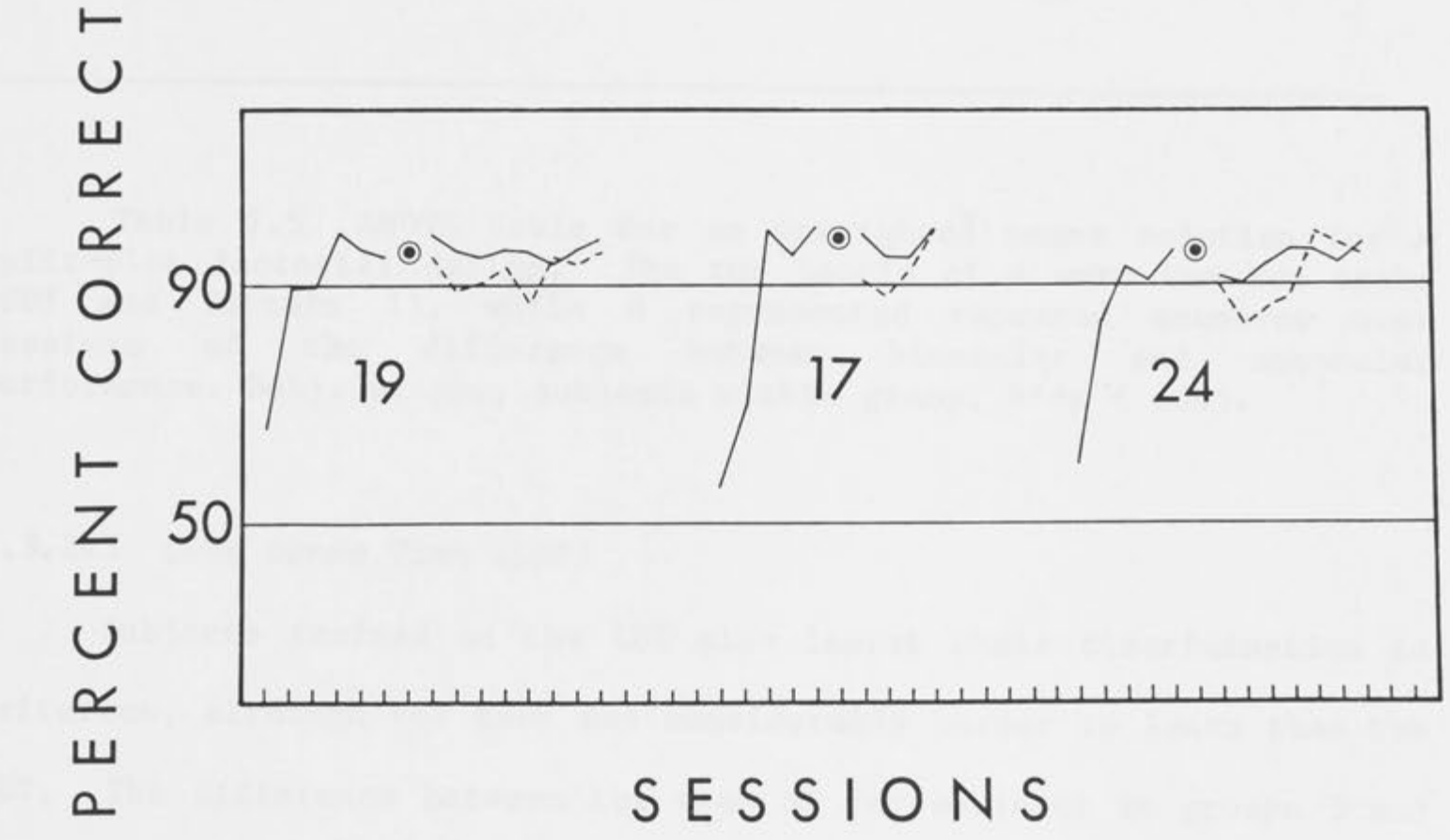


Figure 2.10 The performance curves both before and during monocular testing on the Pattern 1 task for the three subjects in group 4 (cf. Figure 2.9).

Source	SS	df	MS	F
A	4,021	1	4,021	23.7***
Subj. w. gp	1,280	7	183	
B	124	3	42	1.2
A x B	192	3	64	1.8
B x Subj. w. gp	730	21	35	

Table 2.5 ANOVA table for an unweighted means solution for a split-plot factorial design. The two levels of A were the two tasks (SDT and Pattern 1), while B represented repeated measures over sessions of the difference between binocular and monocular performance. Subj. w. gp., subjects within group, ***$p < .005$.

2.3.2.3 *Less Dense Task (LDT)*

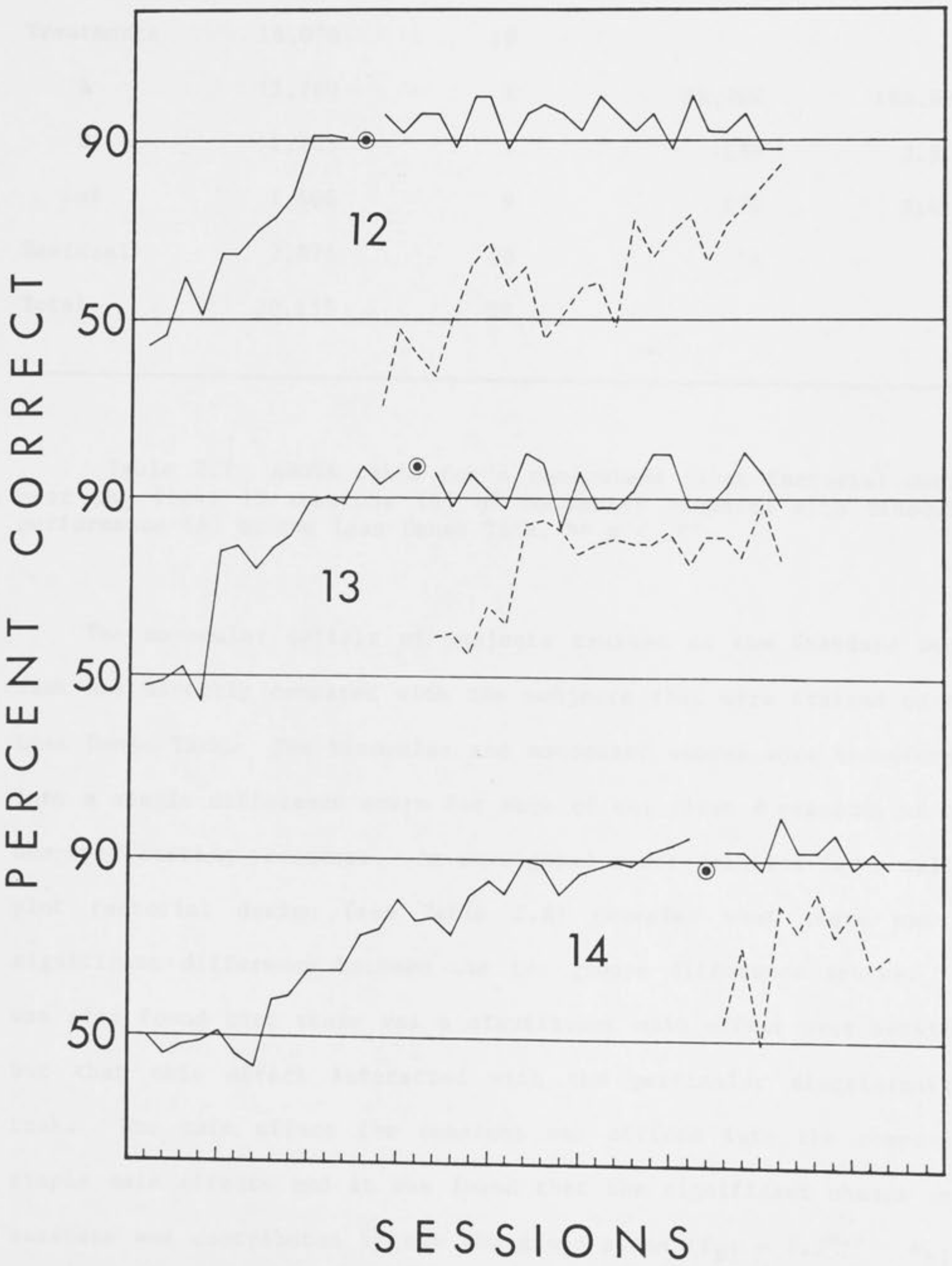
Subjects trained on the LDT also learnt their discrimination to criterion, although the task was considerably harder to learn than the SDT. The difference between the mean SN for subjects in groups 3 and 5 (see Table 2.6) was significant ($t = 3.8$, $p < .005$, $df = 8$).

It can be seen from Figure 2.11 that introduction of monocular testing severely retarded performance and no subjects attained criterion even after extended training. A randomized block factorial design was employed to compare monocular with binocular performance over the first 10 sessions of the one-eyed testing procedure. The resultant ANOVA table is shown in Table 2.7. Again there was a highly significant difference between the two treatments, which remained constant over the 10 sessions analysed.

Group 3 Standard Depth Task (SDT)				Group 4 Pattern 1				Group 5 Less Dense Task (LDT)			
Subject	SN	SL	(r)	Subject	SN	SL	(r)	Subject	SN	SL	(r)
40	18	2.67	(.93)	19	6	4.97	(.77)	12	12	4.52	(.96)
50	6	7.11	(.84)	17	5	11.44	(.89)	13	15	3.80	(.91)
9	9	7.45	(.95)	24	5	7.69	(.85)	14	31	1.75	(.95)
11	13	3.27	(.87)								
8	16	2.87	(.94)								
37	10	5.53	(.92)								
Mean	**12**	**4.8**	**(.91)**		**5.3**	**8.03**	**(.84)**		**19.3**	**3.36**	**(.94)**
S.E.		0.9	(.02)		0.3	1.88	(.04)		5.9	.83	(.02)

Table 2.6 Parameters of the initial acquisition of the three discriminations; SDT, Pattern 1 and LDT; SL, learning rate indicated by the slope of a fitted regression line; SN, number of sessions to criterion; SE, standard error of the mean.

Figure 2.11 The performance curves both before and during monocular testing on the less dense task (LDT) for group 5 subjects (cf. Figure 2.9).


PERCENT CORRECT
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SESSIONS

Source	SS	df	MS	F
Blocks	1210	2	605	8.0**
Treatments	16,070	19		
A	12,760	1	12,760	168.6**
B	1,703	9	189	2.5
AxB	1,606	9	179	2.4
Residual	2,876	38	76	
Total	20,155	59		

Table 2.7 ANOVA table for a randomized block factorial design over the first 10 sessions (B) of monocular compared with binocular performance (A) on the Less Dense Task, ** $p < .01$.

The monocular deficit of subjects trained on the Standard Depth Task was directly compared with the subjects that were trained on the Less Dense Task. The binocular and monocular scores were transformed into a single difference score for each of the first 8 sessions of the one-eyed testing procedure. An unweighted means solution for a split-plot factorial design (see Table 2.8) revealed that there was no significant difference between the two groups difference scores. It was also found that there was a significant main effect over sessions but that this effect interacted with the particular discrimination task. The main effect for sessions was divided into the composite simple main effects and it was found that the significant change over sessions was contributed by the LDT group alone ($F_{B1} = 1.2^{n.s.}$; $F_{B2} = 10.2$, $p < .01$).

In simple terms the analysis reveals that firstly there is no difference in monocular performance relative to binocular between subjects trained on the SDT and those trained on the LDT. Secondly, the difference scores change over sessions for subjects trained on the LDT more so than those trained on the SDT, that is, group 5 subjects attain a relative improvement in their monocular scores over the first 8 sessions of monocular testing, while group 3 subjects do not.

Source	SS	df	MS	F
A	165	1	165	.18
Subj. w. gps	6,562	7	938	
B	2,498	7	357	6.3***
AxB	2,034	7	291	5.1***
B x Subj.w.gps	2,794	49	57	

Table 2.8 ANOVA table for a split plot factorial design with unweighted means solution. The two levels of A were the two tasks (SDT and LDT) while B represents repeated measures over sessions of the difference between binocular and monocular performance, ***p < .005.

2.3.3 Relative Depth Task (RDT)

The percentage correct scores obtained on the transfer test from the SDT to the RDT are shown in Figure 2.13. Transfer was immediate in 3 of the 4 cases. The remaining subject (40) was only disturbed by the change in the negative stimulus (S-) for 3 sessions, after which criterion performance was reinstated. In contrast, all subjects performance fell to chance levels of responding (45.8% - 54.2%) when the standard control was introduced for a single session. The easy transfer from the SDT to the RDT indicates quite clearly that the two

depth stimuli (D10 and D10 inverted) were discriminable and hence distinct.

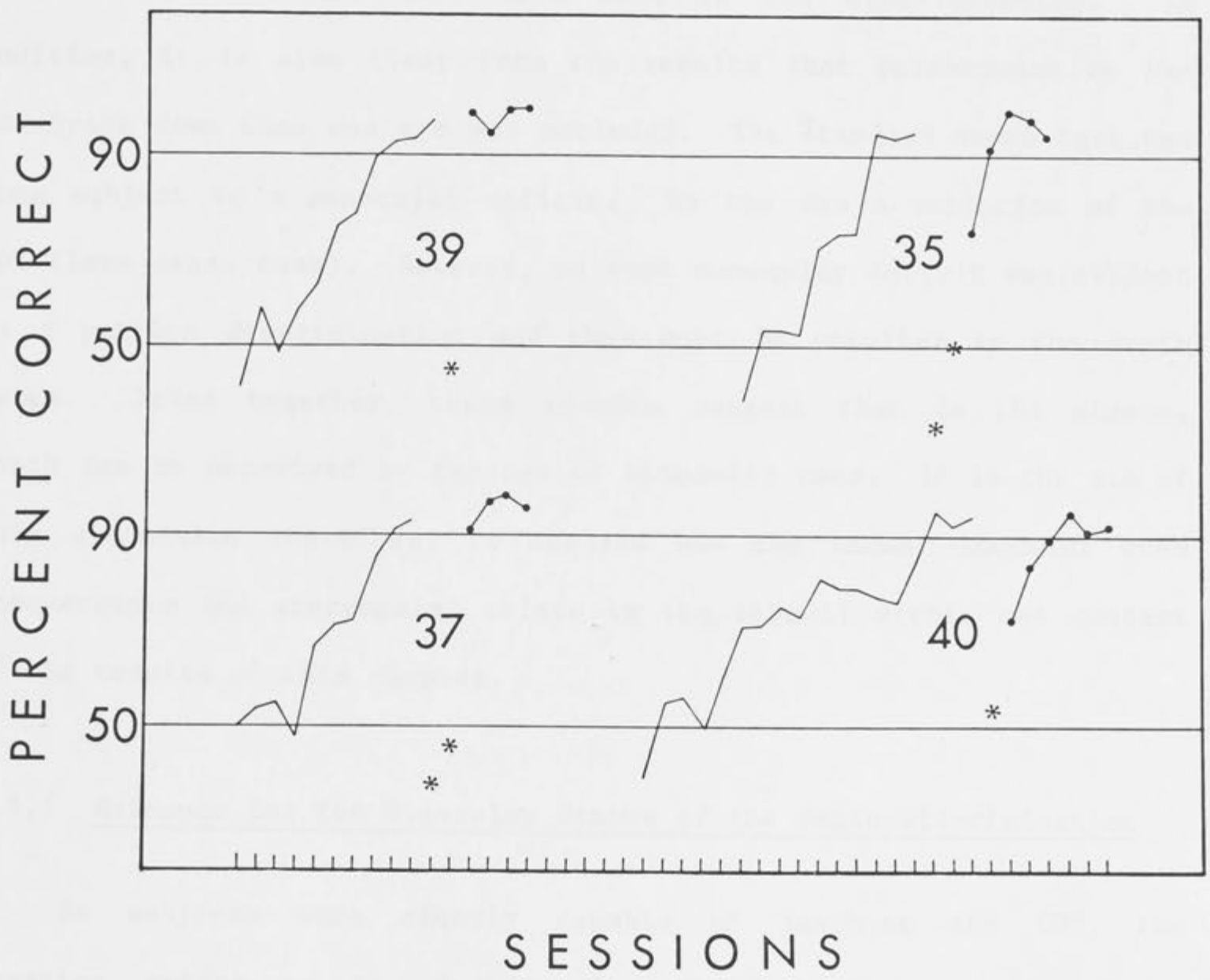


Figure 2.13 Initial acquisition of the standard depth task and subsequent transfer to the relative depth task (⌒) by subjects in group 6. Performance on the standard control indicated by * .

2.4 DISCUSSION

The pigeon is clearly capable of discriminating between a depth and a non-depth stimulus (standard depth task), or indeed between two depth stimuli which only differ in the direction of a displaced circle with respect to the background (relative depth task). Due to the nature of the Frisby depth stimulus, the rapid and almost linear rate of acquisition of the standard depth task (SDT) is suggestive in itself that binocular cues were used in the discrimination. In addition, it is also clear from the results that performance on the SDT broke down when one eye was occluded. The standard depth task was thus subject to a monocular deficit. So too was a variation of the SDT (less dense task). However, no such monocular deficit was evident on a pattern discrimination and thus must be peculiar to the depth tasks. Taken together, these results suggest that in the pigeon, depth can be perceived by the use of binocular cues. It is the aim of this discussion therefore, to analyse how the known binocular cues (convergence and stereopsis) relate to the stimuli within the context of the results of this chapter.

2.4.1 Evidence for the Binocular Status of the Depth Discrimination

As subjects were clearly capable of learning the SDT, the question arises as to whether the discrimination was based on binocular cues to depth. Although there were strong binocular cues present in the depth stimulus, it was possible that subjects only used subtle monocular cues, such as motion parallax, accommodation or monocular cues arising at the edges of the displaced circle. However, there are a number of reasons why the depth discrimination was made principally by the application of binocular cues.

2.4.1.1 *The Monocular Deficit*

When one eye was occluded, performance on both the SDT and the more difficult less dense task (LDT) was severely retarded. This inability to discriminate depth from non-depth efficiently under monocular conditions was not a reflection of some non-specific effect of occlusion of one eye, as no decrements in performance were seen on the pattern 1 discrimination. This latter task was composed of the elements of the depth stimulus but since they were only presented in a single plane, no binocular cues were relevant to the discrimination.

It may be argued that the lack of a monocular deficit in the pattern 1 task was simply a function of the difference in the initial acquisition curve rates. Thus, since the SDT required more sessions on average, and had a slower rate constant than was present in the pattern 1 group, it might be expected that a pattern task equated for 'difficulty' with the SDT would show a similar monocular deficit. That is, the easier the task, the less the observed deficit. If this were true, however, a more difficult task than the SDT might also be expected to produce an even greater monocular deficit, or, if already at baseline, at least the same monocular deficit. The LDT was harder to learn that the SDT, as evidenced by the significantly slower learning curves. Yet, the initial monocular deficit improved at a faster rate than that seen in the SDT. Furthermore, within the SDT subjects, there was no correlation of the size of the initial monocular deficit with parameters of the initial acquisition curves (number of sessions taken to learn the task, SN, and the slope of the acquisition curve, SL) which indicate task difficulty. Hence it is unlikely that the easier the task was to learn, the less the observed monocular deficit.

Rather, it would seem that the performance decrement observed with monocular occlusion was a function of the specific nature of the depth discrimination. It occurred because subjects had learned the task relying heavily upon binocular cues which became unavailable under monocular conditions. With one eye covered, each bird was forced to rely only upon monocular cues to depth. That this was not easy was evidenced by the poor and highly variable monocular performance, even after extended training. The monocular cues often required movement of the head or eyes and were thus dependent upon secondary processes in order to provide a link between the conditioned and unconditioned stimuli.

2.4.1.2 *Relative Depth Task*

Further evidence for the binocular status of the depth discriminations arises from the fact that the pigeon could distinguish between a circle placed in front of the plane of a surround from a situation in which the circle was behind the plane of the surround. Since both S+ and S- in the relative depth task (RDT) contained two planes of focus, it cannot be argued that the SDT was based simply on the monocular cue of accommodation. Similarly, motion parallax cannot have provided the appropriate cue as it too was a function of both S+ and S- in the RDT.

2.4.2 The Binocular Cues to Depth

Classically, the binocular cues to depth are convergence and stereopsis. Such a distinction appears to imply independence and it is generally regarded, at least in the human visual system, that convergence acting alone is not a very effective cue to depth. Thus one may be led to conclude that stereopsis was the only effective

binocular cue used by the pigeons in the SDT discrimination. Such a conclusion is naive, however, as retinal disparity and convergence are intimately linked both physically and geometrically. Secondly, although convergence alone may be an inaccurate cue to depth in humans, it must be considered in the context of the pigeon visual system.

2.4.2.1 *The Relationship between Convergence and Stereopsis*

In the human visual system, the basic convergence requirement is fulfilled through accommodative convergence, thus providing the gross adjustments for the position of the eyes. Acting alone, accommodative convergence does not provide binocular single vision. Fusional vergence movements provide the fine adjustments needed, the stimulus being disparate retinal imagery. The relationship between binocular disparity and the angle of convergence can be seen geometrically in Figure 2.14. The binocular disparity of one point (R) with respect to another (L) is simply the convergence angle of the first minus the convergence angle of the second ($\theta_R - \theta_L = \gamma_L - \gamma_R$).

The binocular disparity associated with two targets provides no information as to the egocentric distance of either target from the observer (D_R or D_L). It is not necessary to fixate each of the targets to perceive them at different distances. Dove (cited by Boring, 1942) reported the definitive experiment that depth can be perceived from disparity in a stereogram illuminated by a short electric spark, too short for any vergence movement to occur during illumination. Wheatstone (1838) and Fender and Julesz (1967) also report stereopsis with stabilized retinal images. Nevertheless, vergence eye movements are needed to bring the stereo images within the critical limits of disparity.

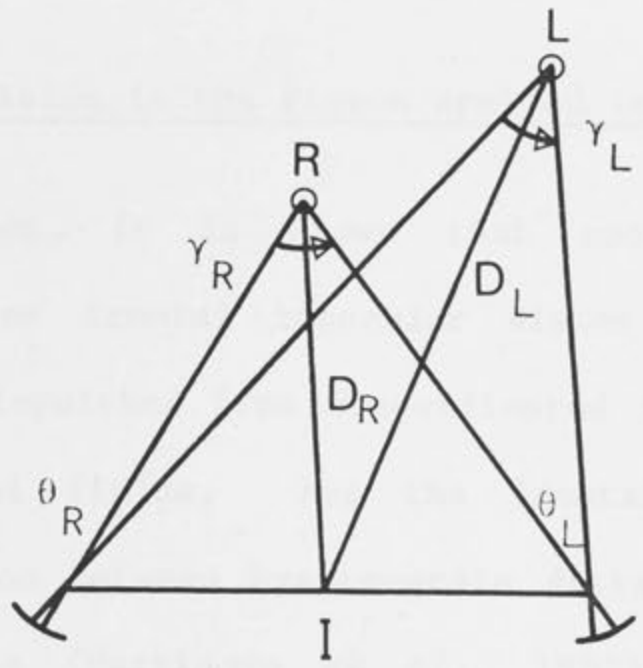


Figure 2.14 Illustration of the stimulus variables convergence angle (γ), horizontal visual angle (θ), and their relation to binocular disparity ($\theta_R - \theta_L$) for two points R and L at egocentric distances of D_R and D_L respectively, from the cyclopean projection centre, I.

2.4.2.2 *Convergence as a Cue for Absolute and Relative Distance*

In the human visual system there is evidence that both perceived depth (Ono and Comerford, 1977; Foley, 1978) and the ratios of perceived egocentric distances (Blank, 1953; Hardy *et al.*, 1953) are effected by changes in the convergence angles of the targets (γ_R and γ_L in Figure 2.14). The effect however, falls far short of the classical hypothesis that we interpret convergence angles correctly and accurately.

In the animal world there are examples of the use of convergence as a cue to absolute distance. For example, manipulation of the convergence angle by prisms placed before the eyes of either the toad (Collett, 1977) or the praying mantid (Rossel, 1983) interferes with the perception of egocentric absolute distance to a prey object. It was not clear from these studies whether the cue to strike was simply a function of the transition from a double to a single image or a direct function of the size of the angle of convergence. However, there are no studies implicating convergence as a cue to relative distance (depth) perception in animals.

2.4.3 Binocular vision in the Pigeon applied to the Depth Stimuli

In the pigeon, it is known that coordinated vergence eye movements occur for frontal binocular vision (Bloch *et al.*, 1981) which can be distinguished from uncoordinated ipsilateral saccades in the lateral visual fields. For the frontal field, there was a negative correlation between eye-to-grain distance during pecking and eye vergence angle (Martinoya *et al.*, 1982). Hence pigeons may possess the basic eye movements which could allow utilization of either stereoscopic and/or convergence cues.

The application of these cues to the depth stimuli is shown in Figure 2.15 in which not only the SDT but also the ability to transfer immediately to the RDT was considered. In Figure 2.15a, it can be seen that absolute convergence angles would not be a sufficient cue unless fixation was approximately in the centre of one of the stimuli. If this occurs then S+ will be directly correlated with the smallest angle of convergence (γ') for both the SDT and the RDT. However, if fixation occurs off-centre, convergence would not provide the appropriate key to the discrimination unless it was combined with pattern recognition. In contrast, retinal disparity provides a cue to depth over a much greater range of stimulus area. The discrimination of the SDT would consist of crossed diplopia versus no disparity (Figure 2.15b), while the RDT would consist of a discrimination of crossed versus uncrossed disparity. Thus S+ would be correlated not simply with the disparity present, but with the direction of the displacement in depth.

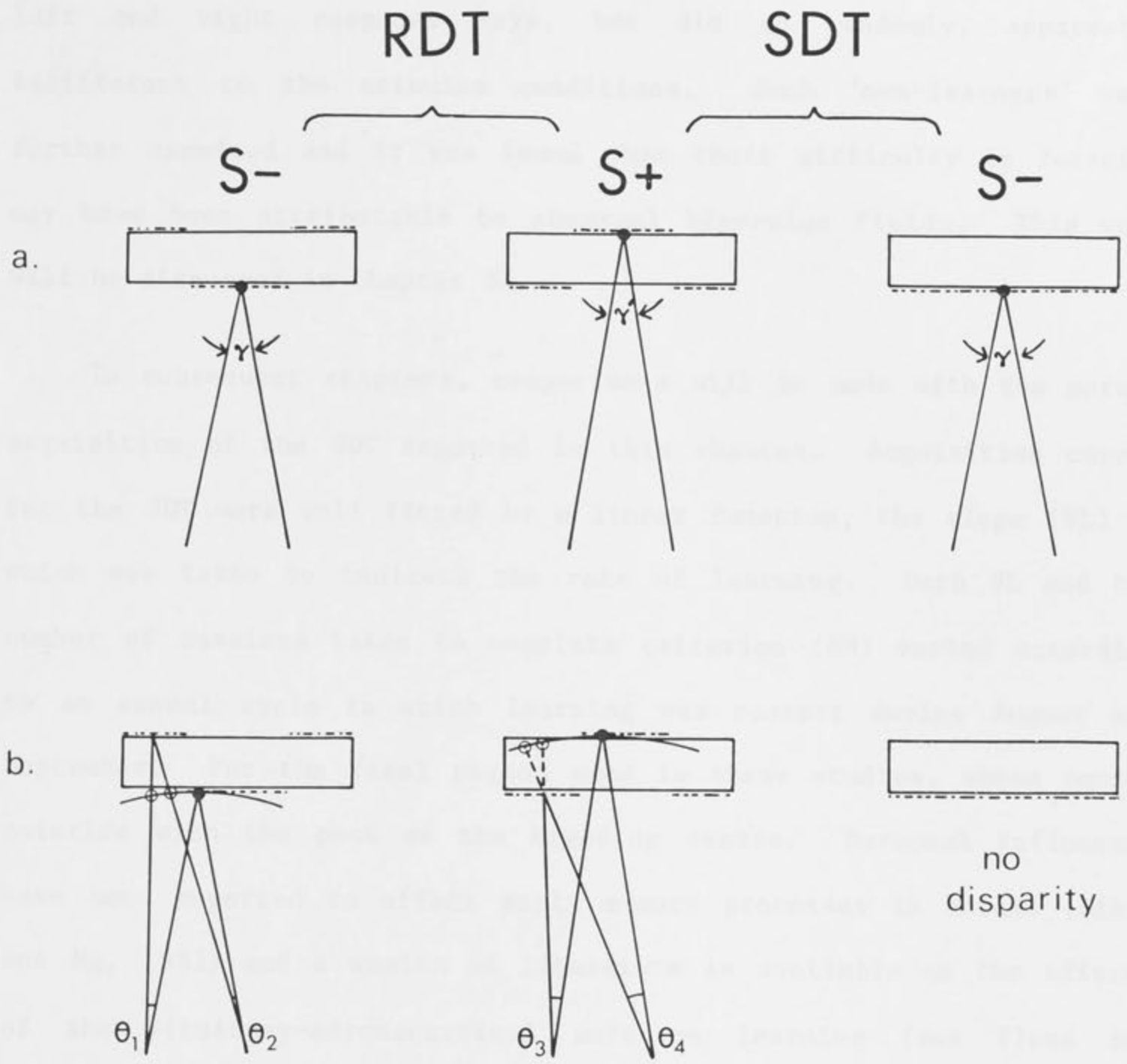


Figure 2.15 a. Absolute convergence angle could serve as the cue for S+ provided fixation occurs near the centre of either stimulus. b. Retinal disparity could also serve as a cue to depth. Fixation is shown as on the circle, thus making S+ a function of crossed disparity and S- a function of either uncrossed or no disparity. Fixation could also be considered as occurring on the surround.

2.4.4 Acquisition of the Standard Depth Task

The results of this Chapter support the hypothesis that during discrimination of the SDT, the pigeon used a binocular cue. However, there was a small population of birds which failed to learn the SDT despite extended training. These birds were capable of pecking the

left and right response keys, but did so randomly, apparently indifferent to the stimulus conditions. Such 'non-learners' were further examined and it was found that their difficulty in learning may have been attributable to abnormal binocular fields. This work will be discussed in Chapter 5A.

In subsequent chapters, comparisons will be made with the normal acquisition of the SDT reported in this chapter. Acquisition curves for the SDT were well fitted by a linear function, the slope (SL) of which was taken to indicate the rate of learning. Both SL and the number of sessions taken to complete criterion (SN) varied according to an annual cycle in which learning was poorest during August and September. For the feral pigeon used in these studies, these months coincide with the peak of the breeding season. Hormonal influences have been reported to affect early memory processes in chicks (Gibbs and Ng, 1983) and a wealth of literature is available on the effects of the pituitary-adrenocortical axis on learning (see Flood and Jarvik, 1976). It would be extreme to suggest that only the particular behaviour pattern under study was subject to the observed cyclic variation. More probably, many, if not all behaviours were effected. Subsequent comparisons with the normal acquisition rates of the SDT will consider this cyclic variation, although it should be noted that overall the mean SN was 10.5 sessions.

2.4.5 Open Questions

Although binocular vision was required for the discrimination of depth from non depth in the SDT, the exact nature of the binocular mechanism is not known. Possibilities have been discussed and the questions remain open as to how finely tuned this mechanism is, and where in the pigeon visual system binocular interaction can occur.

CHAPTER THREE

THE ROLE OF THE VISUAL WULST IN BINOCULAR DEPTH PERCEPTION AND DEPTH ACUITY IN THE PIGEON

CONTENTS

3.1 INTRODUCTION

3.1.1 A Brief Account of the Avian Visual System

In all avian species studied, the optic nerve of each eye crosses almost completely at the optic chiasm and thus primary retinal targets only receive projections from the contralateral eye (Cowan *et al.*, 1961; Karten and Nauta, 1968; see however Takatsuji, 1982). Hence, binocular neural interaction of the two eyes must occur via secondary or subsequent visual projections.

In the pigeon, primary retinal afferents terminate contralaterally in a complex of nuclei in the dorsal thalamus (OPT), the ventral geniculate nucleus (GLv), supraoptic nucleus (SO), parts of the pretectal complex, the ectomammillary nucleus (EM), the mesencephalic lentiform nuclei (LM) and most extensively in the optic tectum (TeO) (Cowan *et al.*, 1961; Karten *et al.*, 1973; Meier *et al.*, 1974; Streit *et al.*, 1980; for a review see Cohen and Karten, 1974). Despite the years of concern with the visual system, surprisingly little is known about the second order projections of many of these structures.

In order to determine a possible neural site in which binocular interaction may occur, it is of interest to note firstly the prominent role of the optic tectum in mediating visual behaviour. The diverse efferent connections of the optic tectum are described in Section 3.1.1.1. The TeO also provides the basis for parallel ascending visual pathways to the telencephalon. There has also been described another ascending system which bypasses the TeO and has been designated as the thalamofugal system. A brief account of the anatomy and the possible functions of each of these two major ascending visual systems are described in Sections 3.1.1.2 and 3.1.1.3 respectively.

It is within the latter system that some evidence suggests that a possible site mediating binocular depth perception may exist (see Sections 3.1.2 and 3.1.3). One of the aims of this chapter is to investigate such a possibility by examining the effect of selective lesions of this particular site on performance measures of the binocular depth task already described.

3.1.1.1 *The Optic Tectum*

The efferent projections of the optic tectum (TeO) are extremely diverse. TeO projects topographically upon the isthmo-optic nucleus which in turn projects topographically upon the retina (McGill *et al.*, 1966a,b; Cowan, 1970) thus providing the basis for a centrifugal system.

The nucleus isthmi, pars parvocellularis (Ipc) and nucleus semilunaris (SLu) also receive highly topographically organized ipsilateral tectal projections (McGill *et al.*, 1966a) and project back upon corresponding portions of the optic tectum (TeO) (Hunt *et al.*, 1975). TeO also projects ipsilaterally to the nuclei listed in Table 3.1 and bilaterally upon the pretectal nuclei, nucleus subpretectalis (SP) and nucleus interstitio-pretecto-subpretectalis (IPS), nucleus rotundus (Rt), and nucleus triangularis (T) (Karten, 1965; Karten and Revzin, 1966; Benowitz and Karten 1976; Hunt and Kunzle, 1976; Reperant *et al.*, 1977) crossing to the contralateral nuclei via the ventral supraoptic decussation (DSO_v) (Hunt and Kunzle, 1976; Reperant *et al.*, 1977) (See Figure 3.1).

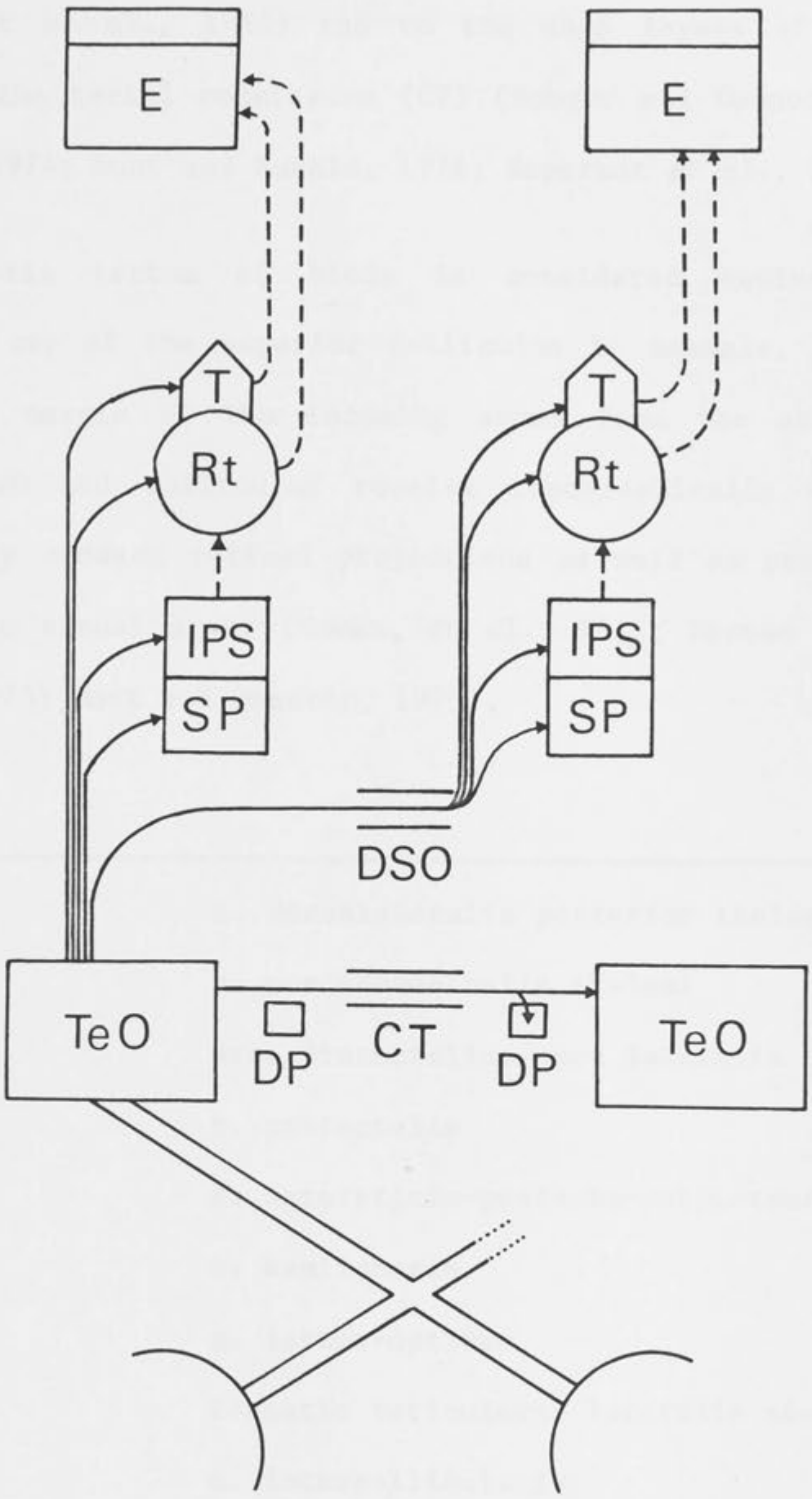


Figure 3.1 Diagramatic representation of the primary (solid arrows) and secondary (dotted arrows) efferent projections of the optic tectum. The known crossed projections pass through the supraoptic decussation (DSO) and the tectal commissure (CT). See Table 3.1 for abbreviations.

TeO also projects to the opposite area pretectalis, pars dorsalis (DP) (Streit *et al.*, 1980) and to the deep layers of the opposite tectum via the tectal commissure (CT) (Robert and Cuenod, 1969; Barth and Felix, 1974; Hunt and Kunzle, 1976; Reperant *et al.*, 1977).

The optic tectum of birds is considered equivalent to the superficial cap of the superior colliculus in mammals, as defined by the ventral margin of the incoming axons from the striate cortex. Both the TeO and colliculus receive topographically organized and predominantly crossed retinal projections as well as projections from telencephalic visual areas (Cowan, *et al.*, 1961; Karten *et al.*, 1973; Graybiel, 1975; Hunt and Webster, 1975).

DLP	n. dorsolateralis posterior thalami
PV	n. posteroventralis thalami
LP	area pretectalis. pars lateralis
PT	n. pretectalis
IPS	n. interstitio-pretecto-subpretectalis
SLu	n. semilunaris
ION	n. isthmo-opticus
FRL	formatio reticularis lateralis mesencephali
LCo	n. intercollicularis
PL	n. pontis lateralis
PM	n. pontis medialis
GLv	n. geniculatus, pars ventralis
Ipc	n. isthmi, pars parvocellularis

Table 3.1 Nuclei which receive afferent projection from the optic tectum.

3.1.1.2 *Tectothalamic Pathways*

The TeO projects to GLv (Voneida and Mello, 1975) which is also in receipt of fibres of the optic tract (Cowan *et al.*, 1961; Karten and Nauta, 1968; Meier *et al.*, 1974) and sends its efferent back to the TeO (Brecha, 1978: see Hodos *et al*, 1982). In addition both Rt and T receive fibres from the TeO, the latter of which receives afferents from SP, itself a recipient of tectal input (Benowitz and Karten, 1976).

Rt appears to be dominated by the visual input from TeO, and Hodos and Karten (1966) and Karten and Revzin (1966) concluded on the basis of anatomical, physiological and behavioural studies, that the Rt represented a major lemniscal terminus of an ascending visual system and designated this as a tectofugal pathway (Karten, 1969; Karten and Hodos, 1970; Nauta and Karten, 1970) (See Figure 3.1).

Such a tectofugal system is recognised in several mammalian forms (e.g. Altman and Carpenter, 1961; Diamond and Hall, 1969; Schneider, 1969) and there are striking similarities between the ascending tectorotundal pathway of birds and the collicular-nucleus lateralis posterior pathway of mammals (Karten, 1969). In mammals, the pulvinar or the lateral posterior nucleus of the thalamus then projects mainly to extrastriate visual areas (Harting *et al.*, 1972; Kaas *et al.*, 1972; Lin *et al.*, 1974; Benevento and Rezak, 1976; Coleman *et al.*, 1977; Curcio and Harting, 1978). The function of this pathway, at least at the collicular level, appears related to visual attention and, in primates, to the control of eye movements (Trevarthen, 1967/68 Schneider, 1969; Schiller and Stryker, 1972; Mohler and Wurtz, 1977).

In birds, both Rt and T also project in parallel pathways to the ipsilateral ectostriatum of the telencephalon (Revzin and Karten, 1966/67; Benowitz and Karten, 1976) which in turn projects to the

ectostriatal belt. Thus the nucleus rotundus and triangularis appear to be the thalamic relays between the optic tectum and the telencephalon (Figure 3.1).

The behavioural effects of lesions in various components of the avian tectofugal system have left little doubt that this pathway is involved in mediating visual discrimination.

Bilateral tectal lesions result in a permanent loss of a pattern discrimination (Hodos and Karten, 1974) and even tiny tectal lesions detrimentally affect performance on an intensity discrimination (Cohen, 1967a). Subjects made to perform a discrimination with the eye contralateral to a unilateral tectal ablation appear blind, and are unable to respond on visual discriminations (Mello, 1968) and appear to depend heavily on tactile cues (Jarvis, 1974). In line with the anatomy of complete decussation at the optic chiasm, little impairment is seen in retention of a visual discrimination (Mello, 1968) or in the acquisition of a left-right discrimination (Binggeli *et al.*, 1963) with the eye ipsilateral to a unilateral tectal lesion.

Bilateral lesions in the Rt, ectostriatum, tecto-rotundal or rotundo-ectostriatal fibres result in deficits in visual intensity and pattern discrimination (Hodos and Karten, 1966; Jarvis, 1974). The extent of impairment on performance of the pattern discrimination was correlated with the size of the lesion. The deficits were characterized by a post-operative return to chance performance yet were *always* followed by an eventual return to high levels of discrimination capacity. Rotundus lesions also result in deficits on colour discrimination problems, although less pronounced than those seen in pattern and visual intensity tasks (Hodos, 1969). The faster rate of recovery may reflect differences in the acquisition rate of the colour task, which was more rapid than that seen for either the

pattern or luminance tasks described above.

Hodos and Bonbright (1974) used psychophysical procedures in conjunction with signal detection theory and obtained threshold measurements for successive brightness differences. Following lesions of Rt or ectostriatum, severe losses in sensitivity on threshold measurements were found.

3.1.1.3 *Thalamofugal Pathway*

Apart from the tectofugal system, there has been described in both birds and mammals a thalamofugal system which is more direct and in the avian brain provides a link between the retina and the telencephalon via a thalamic synapse system.

The complex of dorsal thalamic nuclei receiving afferents from the retina has been designated the nucleus opticus principalis thalami, or OPT complex (Karten *et al.*, 1973). The OPT complex includes the nucleus lateralis anterior (LA), nucleus dorsolateralis anterior, pars magnocellularis (DLAmc); and the dorsal and ventral components of the nucleus dorsolateralis anterior, pars lateralis (DLLd and DLLv).

With the exception of the virtually totally crossed nature of the retinothalamic projection, the OPT complex bears several similarities to the dorsal nucleus of the lateral geniculate (dLGN) of mammals, particularly with respect to its subsequent projections. In mammals, efferents from the dLGN terminate in the striate cortex (Wilson and Cragg, 1967; Garey and Powell, 1971; Kaas *et al.*, 1976; Wilson *et al.*, 1977). In the cat and monkey, direct geniculate projections have been found to extrastriate areas as well as to the striate cortex (Garey and Powell, 1967; Wilson and Cragg, 1967; Graybiel, 1972; Le Vay and Gilbert, 1976; Hollander and Vanegas, 1977; Yukie and Iwai, 1981;

Bullier and Kennedy, 1983).

The telencephalic target of the OPT complex in birds is the 'visual' Wulst, the posterior portion of a bulge on the dorsal surface of the avian brain (Karten *et al.*, 1973). The visual Wulst is a multilaminated structure consisting of four prominent layers: the hyperstriatum accessorium (HA); a granular cell layer designated the nucleus intercalatus hyperstriati accessorii (IHA); the hyperstriatum intercalatus suprema (HIS) and a deeper lying layer of large cells, the hyperstriatum dorsal (HD) (Karten *et al.*, 1973) (See Figure 3.2).

In contrast to the behavioural deficits observed after lesions in every component of the tectofugal pathway in birds, discrimination behaviour appears extremely resilient to lesions of the various components of the thalamofugal system. While initial results (Zeigler, 1963) indicated that hyperstriatal damage to the Wulst and the immediately underlying areas of HD may impair brightness and pattern vision, subsequent investigators have found little impairment in simple colour, brightness and pattern discriminations (Pritz *et al.*, 1970; Hodos *et al.*, 1973) with lesions restricted to the visual Wulst. Stettner and Schultz (1967) reported that lesions that were generally restricted to HA and HD had no effect on the acquisition of pattern discimination in quails, but destruction of HA impaired the quails' ability to *reverse* the learned discrimination. Indeed, the deficiencies that may be found from Wulst lesions are more apparent when using a successive discrimination paradigm (Zeigler, 1963) where they can perhaps be attributed to interference with response inhibition processes rather than discrimination capabilities (Macphail, 1969).

Salzen and Parker (1975) suggest that the hyperstriatum is concerned with arousing and maintaining orientation within a stimulus

field. Parker and Delius (1980) support this suggestion with the finding that percent correct scores give no indication that a colour discrimination was impaired by Wulst lesions, yet these pigeons exhibit significantly longer choice latencies. Furthermore, Cohen and Pitts (1967) report that stimulation of IHA resulted in highly specific directional orientation of the head, and concluded that the hyperstriatum may be involved in mediating visual orientation responses of the head and body (Cohen, 1967b). Triesman (1969) went so far as to suggest that a possible function of the thalamofugal system concerns selective attention.

Although lesions of the thalamofugal system have little effect on relatively easy discriminations, losses in sensory capacity can be revealed using stimuli that approach the threshold of discriminability. Thus, both OPT lesions (Hodos and Bonbright, 1974) and Wulst lesions (Pasternak and Hodos, 1977) result in sensory deficits in luminance difference thresholds. When the OPT complex is lesioned in addition to Rt, thus severing the thalamic relays of both the tectofugal and thalamofugal systems, increased deficits occur on a pattern discrimination when compared with Rt lesions alone (Hodos *et al.*, 1973). An eventual return to pre-operative performance levels was still obtained thus indicating that brain stem structures are sufficient to maintain visual pattern discrimination given adequate training.

Hodos *et al.* (1973) suggest that the coarse discrimination procedures used in other studies may not have detected impairment because the residual sensory capacity of the visual system was sufficient for successful performance of coarse discrimination tasks. Such a conclusion is further supported by the finding that deficits occur when using the eye contralateral to a unilateral

nucleus dorsolateralis lesion, but only on the acquisition of a difficult pattern discrimination (Maier and Tanaka, 1973). Nevertheless, the subtle effect of lesions in the thalamofugal system when compared to the tectofugal system is also shown in this study, as pigeons with lesions of the nucleus rotundus showed deficits on *both* an easy and a difficult pattern discrimination.

On the basis of physiological and anatomical evidence, an additional function has been ascribed to the 'visual' Wulst - that of binocular vision processing.

3.1.2 Binocular processing in the striate cortex

Several authors have noted the similarity between the avian 'visual' Wulst and the striate cortex of mammals (Nauta and Karten, 1970). Both receive retinotopic visual inputs from retinorecipient thalamic cell groups (Karten *et al.*, 1973; Pettigrew and Konishi, 1976a). Both have similar efferent projection targets, including the retino-recipient thalamic cell group which projects to the telencephalon, the ventral geniculate nucleus, tectum and several visual pretectal nuclei (Karten *et al.*, 1973; Rodieck, 1979).

The two principal functions of the striate cortex in the cat and macaque are to combine the inputs from the two eyes to yield a fused image and analysis of the visual world with respect to orientation of local contours (Hubel and Wiesel, 1962, 1968). Associated with these functions are two independent overlapping columnar systems, one for ocular dominance and one for stimulus orientation (Hubel *et al.*, 1978). An additional function suggested for the striate cortex is to analyse retinal image disparity for stereoscopic depth perception.

It seems generally agreed that some striate cortical neurons have receptive fields with demonstrably non-zero binocular disparity but because of the difficulty of monitoring eye positions accurately, it remains controversial whether their incidence is low (Hubel and Wiesel, 1970, 1973; Clarke *et al.*, 1976; Hughes, 1977; Clarke and Whitteridge, 1978) or rather high (Barlow *et al.*, 1967; Nikara *et al.*, 1968; Joshua and Bishop, 1970; Poggio and Fisher, 1977).

It should be noted that many cells whose receptive field disparities are classified as experimentally indistinguishable from zero might still have functionally significant non-zero disparities. Many striate cortical neurons in the cat are sharply tuned for disparity in that they respond well during binocular stimulation only within a narrow range of disparities much smaller than the overall receptive field dimensions (Pettigrew *et al.*, 1968). Sharp disparity tuning has been reported for many cells in the striate cortex of the macaque while the animal is unanaesthetized (Poggio and Fisher, 1977), but not during anaesthesia (Hubel and Wiesel, 1970). Once again it has been difficult to determine what percentage of disparity-tuned cells have optimal disparities different from zero. Since disparity-tuned cells that prefer stimuli in exact retinal correspondence might be involved in fusion rather than actual depth perception, the functional significance of disparity tuning in the striate cortex remains uncertain.

In contrast, there is little doubt that the extrastriate cortical regions do contain disparity tuned, binocular-only cells (Hubel and Wiesel, 1970; Poggio and Fisher, 1977).

An important means for assessing the overall role of particular cortical areas in visual perception has been to observe the behavioural deficits after restricted cortical lesions. After

ablation of areas 17, 18 and part of 19 in the cat, Kaye *et al.* (1981) found that the animals were unable to solve a depth discrimination in which subjects were required to leap to the nearer of two platforms (see Section 1.5.7.1). Preoperative binocular superiority of the cats' threshold performance was abolished, and Kaye *et al.* (1981) concluded that ablation of striate and extrastriate cortical regions eliminated capacity for stereoscopic vision. This implies that the parallel visual pathways to other cortical areas (Sprague *et al.*, 1977) which can mediate moderately high visual acuity and form vision after ablation of visual cortex nevertheless by themselves cannot process retinal disparity (Berkely and Sprague, 1979). Furthermore, these authors claimed that the lesioned cats were also extremely limited in their capacity to evaluate not only binocular but also monocular cues to depth.

3.1.3 Binocular processing in the Visual Wulst

It is known that a bilateral projection occurs from the OPT complex to the visual Wulst in a variety of birds. Such an organization has been observed in the pigeon (*Columba livia*) (Miceli *et al.*, 1975) and the owl (Karten *et al.*, 1973). A similar pattern was also observed in the feral pigeons used in this thesis (McFadden and Wild, unpublished observations). Miceli *et al.* (1975) also report that a bilateral thalamic-hyperstriatal pathway exists in the chick, duck, herring gull and jackdaw. There are conflicting reports regarding the sites of termination of thalamic projections and it is difficult to assess to what degree the differential distribution of labelled neuron populations in the Wulst is attributable to intrinsic synaptic organisation. Most authors would agree however that DLLd is the site of bilateral projections, mainly to the lateral part of IHA. It has also been suggested that regions of HA also receive

bilateral projections from DLLd, while DLLv sends ipsilateral afferents to HD or medial HIS (Hunt and Webster, 1972; Karten *et al.*, 1973; Meier *et al.*, 1974; Miceli *et al.*, 1975; Watanabe, 1982).

The highest density of retinal fibers terminating in DLL are located in the ventral portion of DLLd (Meier *et al.*, 1974; Miceli *et al.*, 1975; Miceli *et al.*, 1979) which corresponds to the area providing bilateral ascending projections. This area also contains neurons with bifurcating axonal connections to the hyperstriatum of both hemispheres (Meier *et al.*, 1974; Miceli and Reperant, 1982) and suggests that the same visual information is transmitted simultaneously to both hemispheres (See Figure 3.2).

Burkhalter *et al.* (1979) reported that DLL receives a retinotopically organized input from retinal ganglion cells in the pigeon. Rostral DLL was found to receive efferents from the temporal half of the retina. Since the binocular portion of the pigeon visual field projects to temporal retina, it is possible that DLL is providing a link in the processing of binocular vision information in the pigeon Wulst. The notion that the retino-thalamo-hyperstriatal pathway plays an important role in the processing of binocular information has been stressed by several authors (Perisic *et al.*, 1971; Pettigrew and Konishi, 1976a,b; Miceli and Reperant, 1982). Perisic *et al.* (1971) distinguished three areas in the pigeon Wulst. One particular area which receives both contralateral *and* ipsilateral input was sandwiched between a dorsally located area receiving input only from the contralateral eye, and a ventrally located area receiving input from the ipsilateral eye.

Revzin (1969) reported retinotopic organization in IHA of the pigeon. A columnar functional organisation was evident when the electrode was inserted perpendicular to IHA. Pettigrew and Konishi

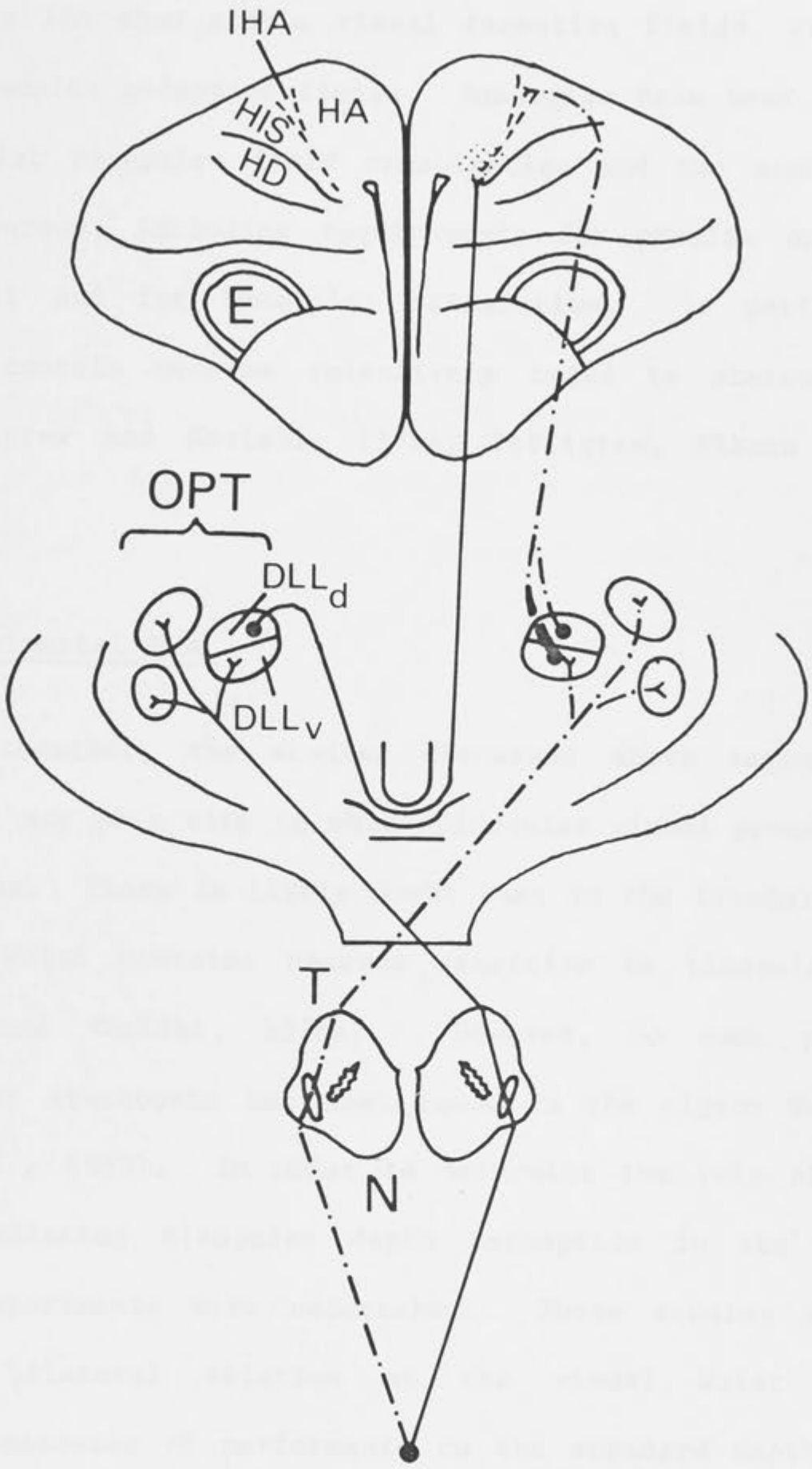


Figure 3.2 Diagramatic representation of a possible pathway involved in binocular visual processing. DLL, nucleus dorsolateralis, pars lateralis; E, ectostriatum; HA, hyperstriatum accessorium; HD, hyperstriatum dorsal; HIS, hyperstriatum intercalatus suprema; IHA, nucleus intercalatus hyperstriati accessorii; OPT, nucleus opticus principalis thalami; N, nasal; T, temporal.

(1976a) have found a similar organisation in the owl and noted that units within IHA show simple visual receptive fields, while HA units have more complex receptive fields. Analogies have been drawn between the owl Wulst receptive field organisation and the mammalian visual cortical neurons, including requirements for precise orientation of edge stimuli and for binocular stimulation. In particular, both structures contain neurons selectively tuned to stereoscopic depth cues (Pettigrew and Konishi, 1976a; Pettigrew, Nikara and Bishop, 1968).

3.1.3 Experimental Aims

Taken together, the studies discussed above suggest that the visual Wulst may be a site in which binocular visual processing occurs in the pigeon. There is little doubt that in the frontally eyed owl, the visual Wulst contains neurons sensitive to binocular disparity (Pettigrew and Konishi, 1976a). However, no such physiological substrate for stereopsis has been found in the pigeon Wulst to date (Frost *et al.*, 1983). In order to determine the role of the visual Wulst in mediating binocular depth perception in the pigeon, the following experiments were undertaken. These studies examined the effect of bilateral ablation of the visual Wulst on various behavioural measures of performance on the standard depth task (SDT) developed in chapter 2.

Firstly, both acquisition and retention of the SDT were examined after bilateral aspiration of the visual Wulst. Several psychophysical studies mentioned in Section 3.1.1.3 have indicated changes in sensory capacity that were not obvious in previous discrimination tests using only coarse stimulus differences (Hodos and Bonbright, 1974; Pasternak and Hodos, 1977). A psychophysical

assessment of sensory performance allows the precise determination of the limits of information processing ability. Thus the behavioural measures chosen in the following experiments not only included acquisition and retention of the standard depth task but also examined absolute psychophysical depth thresholds.

The second aim of the experiments reported below was to assess the limit of sensory capacity of depth perception in normal birds. Such an experiment was clearly necessary in order to evaluate losses in sensory capacity after Wulst lesions. However, normal depth thresholds are also of interest in their own right as they provide an estimate of binocular depth acuity. This allows comparison with stereoacuity both in humans and other animals, in addition to the pigeons normal spatial frequency acuity.

3.2 METHODS

The following methods Section is divided into two parts. The first deals with the procedure employed for all the experiments with pigeons. The second Section describes the adaptations used to measure psychophysical depth thresholds in humans.

A. Pigeon Methods

3.2.1 Subjects

Twenty five feral pigeons reduced to 80% of their *ad-libitum* weight (see Section 2.2.1) were divided into the groups shown in Table 3.2. Note that some subjects were used for more than one experimental manipulation.

Group Number	Group Description	Subject Identification	
		A. Wulst lesioned	B. Non lesioned
1	SDT Acquisition	41 42 43 44 28 29 30	17* 19* 24* See Section 2.3.1
2	SDT Retention	32 33 36 38	15* 16* 18* 20*
3	Pattern 2 Retention	28 29 30	61 58
4	SDT Thresholds	32 33 28 29 30	35 37# 39 40 49 (10 11)

Table 3.2 Assignment of subjects to groups. Each group is divided into two parts. Part A subjects were given bilateral aspiration of the visual Wulst prior to the behavioural test indicated under group description. Part B subjects were either subjected to a sham operation (*) or were given no surgical treatment. One subject in group 4 (#) was also tested on psychophysical SDT thresholds with one eye occluded after the normal binocular measures had been completed.

3.2.2 Apparatus

For groups 1-3 in Table 3.2 the apparatus was as described in Section 2.2.2. The apparatus for threshold testing (group 4) was identical to that described in Section 2.2.2, except that the moveable plate (see Figure 2.2) was fixed at 3cm behind the pecking key plate. An oblong tunnel of white interior was positioned between the two plates (A and B in Figure 2.2) and directly around the pecking keys. The tunnel proportions were 15 x 8.5 x 3cm.

3.2.3 Stimuli

3.2.3.1 *Standard Depth Task (SDT)*

The stimulus used for the SDT acquisition and retention groups (1 and 2) have been described previously in Section 2.2.3.1.

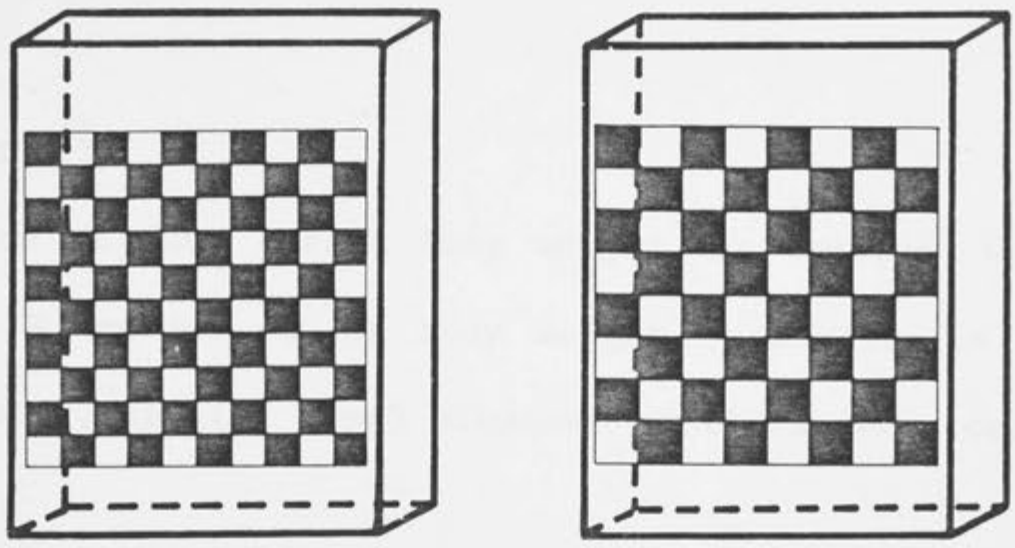
3.2.3.2 *Pattern 2*

The stimuli used for the pattern 2 retention group (group 3) has not yet been described. The stimulus set consisted of two stimuli in which S+ = P2 and S- = CP2.

P2: The pattern 2 positive stimulus consisted of an 10 x 10 checkerboard pattern 45 x 45mm mounted onto the front of an optically clear piece of glass 6mm thick. This pattern can be seen in Figure 3.3(a).

CP2: The control pattern 2 stimulus consisted of a 8 x 8 checkerboard pattern 45 x 45mm and mounted as for S+ (See Figure 3.3.(b)).

The total area of black was equal in both S+ and S-. The stimuli differed only in the size and total number of individual squares making up the checkerboard pattern.



a b

Figure 3.3 The pattern used for the (a) positive and (b) negative stimulus set for the Pattern 2 task.

3.2.3.3 *SDT Threshold*

The stimuli used for threshold testing were based on the SDT already described and consisted of a series of stimulus pairs where D_i = S+ and CD_i = S-.

D_i: The depth stimulus was identical to D10 (see Section 2.2.3.1) except that the thickness of the glass was equal to i. The set of values of i used were [10, 6, 4, 3, 2.5, 1.88, 1, .67, .2, .1] mm.

CD_i: The control depth stimulus was identical to CD10 (see Section 2.2.3.1) except that the thickness of the optically clear glass was equal to i mm as above.

3.2.4 Anaesthetic Agents

Intramuscular injections of either a cyclohexamine anaesthetic (Ketamine) or a barbiturate (Pentathesin[2]) were used to induce profound analgesia.

3.2.4.1 *Ketalar*[2]

Ketamine at 22mg per kg body weight was combined with Xylazine (Rompun[3]) at 4.4mg per kg of body weight. Anaesthesia was induced within 5 minutes, lasting 30-45 minutes. Full recovery occurred after 2 hours.

3.2.4.2 *Pentathesin*[2]

A formulation of pentobarbitone 2%, chloral hydrate 8%, magnesium sulphate 4% in propylene glycol-alcohol-water was injected at a dose rate of 3.5mls per kg of body weight. Complete anaesthesia was induced within 20 minutes and surgical levels lasted up to 1.5 hours. However, the effect was generally variable and birds seemed particularly sensitive during the breeding season.

3.2.5 Surgery

After complete anaesthesia had been induced by one of the above agents, the bird's feathers overlying the ear canal were clipped and the subject was placed in a stereotaxic head holder. The head was positioned such that the horizontal skull axis was 45° to the vertical instrument axis as described in the atlas of Karten and Hodos (1967). The feral pigeons used in the following studies were smaller than the White Carneaux pigeons (*Columba livia*) used to make the standard atlas. Hence, in order to find a particular anterior-

[2]Trade name

posterior (AP) or dorsal-ventral (DV) coordinate, the atlas reading was proportionally reduced by approximately 8%. All AP and DV values reported in this text are with respect to the atlas coordinates.

After a midline skin incision, a plate of bone overlying the Wulst from A13.25 - A7.25 and ML ± 4.0 was removed and kept moistened with saline. The dura was carefully retracted except over the midsaggital sinus. For subjects undergoing Wulst lesions, the sinus was cauterized at both exposed extremes. Two large blood vessels were generally found to feed into this sinus from either side at the posterior end of the Wulst and were also coagulated. Bilateral ablations of the exposed Wulst were performed by aspiration through a glass pipette. Gelfoam was used to control any bleeding, and the piece of bone plate was replaced and secured with a cross of dental cement. The wound was then cleaned and stitched with silk sutures.

The four sham operated subjects in group 2 underwent the same procedure (including cauterization) but no brain tissue was intentionally removed. At the completion of surgical manipulations, subjects were placed in a warm recovery box with water freely available.

3.2.6 Behavioural Procedure

3.2.6.1 *Depth Acquisition (Group 1)*

$1A_n$ (Subjects 41-44): When the pigeons reached 80% of their *ad-libitum* weight, they underwent autoshaping as described in Section 2.2.4.1. The day following this preliminary training all birds in group 1A received a bilateral lesion of the Wulst. Discrimination training on the SDT commenced after a 5-7 day recovery period.

$1A_e$ (Subjects 28-30): These three subjects in group 1A were also

trained on the SDT after a bilateral lesions of the Wulst. However, these subjects were first tested on the retention of a pattern discrimination (see Section 3.2.6.2 below). Hence the first session of discrimination training on the SDT was delayed until 13-19 days after surgery.

1B (Subjects 17, 19 and 24): Group 1B consisted of three subjects who had been given a sham operation and allowed 5-7 days recovery before being tested for acquisition of the SDT.

At the completion of behavioural testing all subjects in group 1 were tested on the standard control session described in Section 2.2.4.2.

3.2.6.2 *Depth and Pattern Retention (Groups 2 and 3)*

The thirteen subjects in the retention groups were first autoshaped and then transferred immediately onto discrimination training (see Section 2.2.4.2). The subjects in the depth retention group were trained with the same stimuli as the depth acquisition group. The pattern chosen for the stimuli of group 3 was based on attempts to equate the learning curve of the depth task with that of a pattern control task. The pattern discrimination was based upon a difference in both the number and size of the component squares.

After criterion had been reached, each subject was tested for one session in which both S+ and S- were equal to CD10 (group 2) or CP2 (group 3) as occurred in the standard control session (see Section 2.2.4.2). Criterion was then re-established on the following session. At the end of the pre-operative training period, subjects were either sham operated or received bilateral aspiration of the Wulst. After a 5-7 day recovery period, all subjects were tested on the same discrimination they had learnt pre-operatively.

3.2.6.3 *Binocular Depth Thresholds (Group 4)*

Depth thresholds were measured in both normal subjects and subjects that had bilateral lesions of the Wulst. Three subjects in the latter group (28, 29 and 30) were lesioned prior to learning the standard depth task (SDT). The remaining two subjects (32 and 33) were lesioned after learning the SDT. For all subjects criterion was well established on the SDT before psychophysical threshold testing began. The procedure was adapted from Hodos and Bonbright (1972).

(i) Pilot study: To find an approximate range of testing a pilot study was first done with subjects 10 and 11. It should be clear that the depth of the image seen in S+ is equal to the thickness of the optically clear glass. Hence, for the standard depth stimulus D10 the depth of the visual image was 10mm. In contrast, the S- always appeared to be in a single plane and the depth of the visual image was approximately zero. Hence the difference in depth between S+ and S- was defined by the thickness of S+. The set of depth differences used were [10, 6, 4, 3, 2, 1, 0] mm. This set defines gradient A. A depth difference of zero was obtained by making both S+ and S- equivalent to CD10.

In the pilot study each subject was given 24 trials (1 block) on each depth difference in decreasing order. Within each stimulus pair, the sequence of stimulus presentation was determined by a quasi-random discrimination sequence. A daily psychometric function of percent correct was plotted as a function of the depth difference. The point of subjective equality (PSE) was taken at the point where the psychometric function crossed the 75% correct line. If more than one crossing occurred the data of that session was discarded. The depth difference equal to the PSE decreased over time until the psychometric function failed to go below 75% on the smallest depth difference

greater than zero. It was clear from this study that the threshold level was less than the smallest depth difference used.

(ii) Final study: The remaining subjects were trained in a manner which allowed a greater range of depth differences to be tested. Before the commencement of psychophysical testing, subjects were trained to generalise from the SDT to a situation in which the stimuli were moved 3cm behind the pecking keys. Once criterion had again been established (3 sessions) psychophysical threshold testing began. Subjects were given one block of trials on each of a decreasing set of depth differences until the subjects' performance fell to chance for two successive blocks. Initially this involved blocks on each depth difference in gradient A. As performance improved over sessions gradient A was expanded to gradient B. Here the set of depth differences were [10, 6, 3, 1, .67, .2, .1, 0] mm. A complete gradient was not initially instigated because of the extinction effect of multiple blocks in which performance fell below chance. As before, the stimulus presentation was determined by a quasi-random discrimination sequence. The daily psychometric function yielded a daily depth difference equal to the PSE. Double crossings of the psychometric function rarely occured and were mostly located during the initial stages of training. Again, such sessions were not included in further analysis.

(iii) Calculation of retinal disparity: If one assumes that the relevant binocular cue utilized in the depth discrimination was based upon the difference between relative convergence angles or retinal disparity, the depth difference corresponding to the PSE can be used to estimate the magnitude of the retinal disparity at threshold.
The retinal disparity γ can be calculated from:

$$= 2 \left[\tan^{-1} \left(a/_{d}\right) - \tan^{-1} a/_{(d + \Delta d)} \right] \text{ degrees of arc}$$

where 2a is the interpupillary distance, d is the distance from the nodal point of the eye to the front face of the stimulus, and Δ d is the depth difference.

The interpupillary distance was measured with calipers individually for each bird. The value of d was calculated in detail with the aid of a frame by frame video analysis of head position during discrimination performance (see Chapter 5B). This analysis found that the decision to peck occurred at a maximum distance of 60mm and a minimum distance of 47mm from the cornea to the pecking key. Adding the distance from the cornea to the nodal point of the eye (3.46mm, see Marshall *et al.*, 1973) and the distance from the key to the front face of the stimuli (38mm) thus makes the value of d between 102mm and 89mm. The latter value is most likely to give the most accurate determination of the retinal disparity (see Section 5.9.2).

(iv) Criterion of stability: Data were collected for each subject until two criteria of stability were met. Firstly, the mean threshold for three successive sessions was less than 20 minutes of arc. This corresponds to the subjects successfully completing gradient A (as in the pilot study) and hence being able to be transferred to gradient B. Secondly, the deviation of the individual thresholds from the mean threshold during *three* successive sessions was less than ± 15%. If a subject stabilized at a mean threshold of greater than 20 minutes of arc, training was continued until a second stabilization criterion was met. Here the deviation of the mean threshold from individual thresholds was required to be less than ± 15% during *five* successive sessions. The last stimulus pair in each daily session contained no stimulus difference (a depth difference

equal to zero). Chance performance on this depth difference ensured that no extraneous cues were present.

3.2.6.4 *Monocular Depth Thresholds*

Monocular depth thresholds were extremely difficult to obtain as subjects were in general unable to discriminate between the stimuli in the SDT with one eye covered (see Section 2.3.2.1). Only one subject (number 37) managed to attain criterion with one eye occluded (see Figure 2.9). This bird's binocular threshold had already been measured 4 months prior to the monocular test described in Section 2.3.2.1. Hence it was decided to measure subject 37's monocular threshold immediately after the monocular training on the SDT shown in Figure 2.9. The binocular and monocular thresholds on the SDT could then be directly compared.

Essentially the same procedure as described above (Section 3.2.6.3) was followed except that all threshold testing was done with one eye occluded, provided the subject attained greater than 90% correct on the first and largest depth difference (10mm). If this proviso was not passed, the session was excluded from the data analysis and the remainder of the session (3 blocks, 24 trials per block) was continued with monocular training on the SDT. The choice of which eye was occluded was alternated from session to session.

Using the video analysis in Section 5.8.4.2 the monocular viewing distance from the cornea to the pecking key was 33.5mm. Adding the cornea to nodal point (3.46mm) and key to stimuli (30mm) distances made the distance, d, from the nodal point of the eye to the front face of the stimulus during monocular threshold testing equal to 75mm. This value of d was used to determine the retinal disparity corresponding to the just noticeable depth differences discernable under monocular conditions by application of the formula given in

Section 3.2.6.3(iii).

3.2.7 Reconstruction of the lesions

At the completion of the post-operative testing period, all birds that had undergone surgery were given a lethal dose of Pentathesin and perfused via the left carotid artery with saline followed by 10% formaldehyde-saline solution. The head was severed from the body, the calcarium removed and the brain *in situ* was submerged in 10% formaldehyde-saline solution overnight. The head was then placed in the stereotaxic instrument and blocked in the stereotaxic plane as described by Karten and Hodos (1967). The brain was removed from the skull and placed in 20% sucrose in fixative (10% formaldehyde-saline) until it sank (24-48 hours). Sections were cut at 40 µm on a freezing microtome and every second section mounted onto gelatinized slides, dried overnight, stained with cresyl violet and coverslipped.

The lesions were reconstructed with the aid of a microprojector. Sections were projected onto drawings of a standard normal brain that had been processed in the same manner as the lesioned specimens. Each brain was examined microscopically for evidence of gliosis and cell loss. The area of damage, defined as missing tissue and severe cell loss, was measured for each of the major divisions of the hyperstriatum (HA, HIS, HD and HV). This was done with the aid of a digitised pad in conjunction with a microprocessor. Area estimation was based on the method of sampled numerical integration of the perimeter with respect to direction. The mean percentage area of three independent readings was used to calculate the percentage damage where:

$$\% \text{ damage of HX} = \frac{\text{area of tissue damage of HX}}{\text{total area of HX in standard brain}} \times 100$$

B. Human Methods

3.2.8 Subjects

The stereoacuity of six human subjects (both male and female) was measured. All subjects were unpractised on the test employed. Their ages ranged from 25-45 years. They wore such optical correction as they would normally need for the viewing distances employed. The mean interocular separation was 65mm (σ = 0.4mm). One subject was blinded in the left eye at 3 years of age and hence, although stereoblind, was experienced in using available monocular cues to perceive depth.

3.2.9 Apparatus

The same operant equipment, stimuli and luminance levels as used for the behavioural pigeon experiments were also employed for the human subjects. However, the stimuli plate was removed from the operant box and set up with a viewing tunnel that was of variable length. A millimeter scale drawn on the tunnel allowed the viewing distance to be determined. The tunnel's maximum length was 130cm, the minimum length 65cm. It was attached directly around the pecking key area. The subject's view of the stimuli was always stationary and each eye's view could be prevented by lowering a flap in front of each eye. This occurred during the one eye tests. All subjects were fitted with earmuffs to eliminate any possible cues from the workings of the apparatus.

3.2.10 Behavioural Procedure

Subjects were given no training prior to the commencement of psychophysical threshold testing. All subjects were instructed to indicate which side had the stimulus with the greater depth. The

procedure was essentially the same as that used for the psychophysical testing of depth thresholds in the pigeon.

At the beginning of each trial the subject was instructed to look down the viewing tunnel. Prior to this command, the stimuli had been moved to an appropriate left or right position according to a quasi-random sequence and the key lights had been switched on. The subject then answered left or right and the corresponding response key was triggered by the experimenter. If the answer was correct a light, visible only to the experimenter, was switched on. Subjects were always informed when their choice had been incorrect. Immediately after the subject had responded, a shutter obscured the view of the stimuli. During this 5 second timeout, the stimuli were repositioned, the keylights were switched on, the shutter was opened and the subject raised his/her eyes to directly view the stimuli. The procedure was then repeated. Unlike the procedure used for discrimination training of the pigeons, no repeat trials were given if the response was incorrect. However, if a subject was unable to make a decision after 11 seconds, the same trial was repeated, and the resultant choice included in the data.

Subjects were given one block of trials (24) on each of a decreasing gradient of six disparity values from 20 - 0.8 secs of arc. This range of disparity values was obtained by using the set of depth differences [6, 3, 1, .67, .2, .1] mm, placed at different viewing distances and applying the formula given in Section 3.2.6.3. The actual values tested were not identical for each subject but were concentrated in the region where a particular subject achieved 60-80% correct responses.

The threshold was defined by plotting the percentage of correct responses as a function of the retinal disparity. The point at which

this psychometric function crossed the 75% correct line was taken as the PSE and the corresponding disparity was taken as the threshold retinal disparity for each subject.

After the psychophysical threshold testing was completed, all normal subjects were tested on the largest disparity value previously used (20 sec of arc) with one eye covered. The choice of eye was random.

Apart from the latter test, the same procedure was implemented for the experienced one-eyed subject, except that the gradient of disparity values tested was increased and ranged from 300 - 25 secs of arc. These values were obtained by using the set of depth differences [10, 6, 3] mm over the range of viewing distances 125 - 65cm.

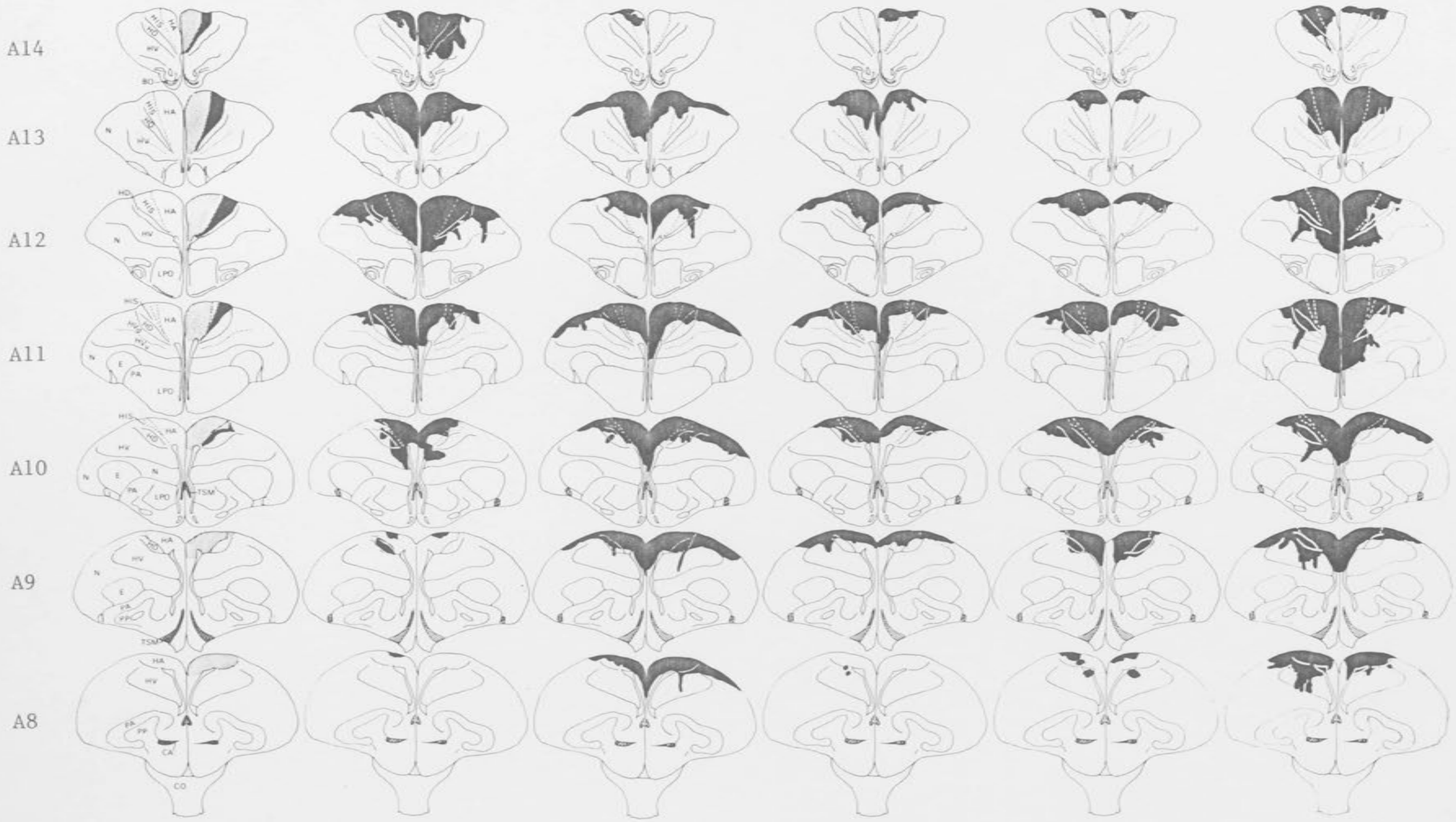
3.3 RESULTS

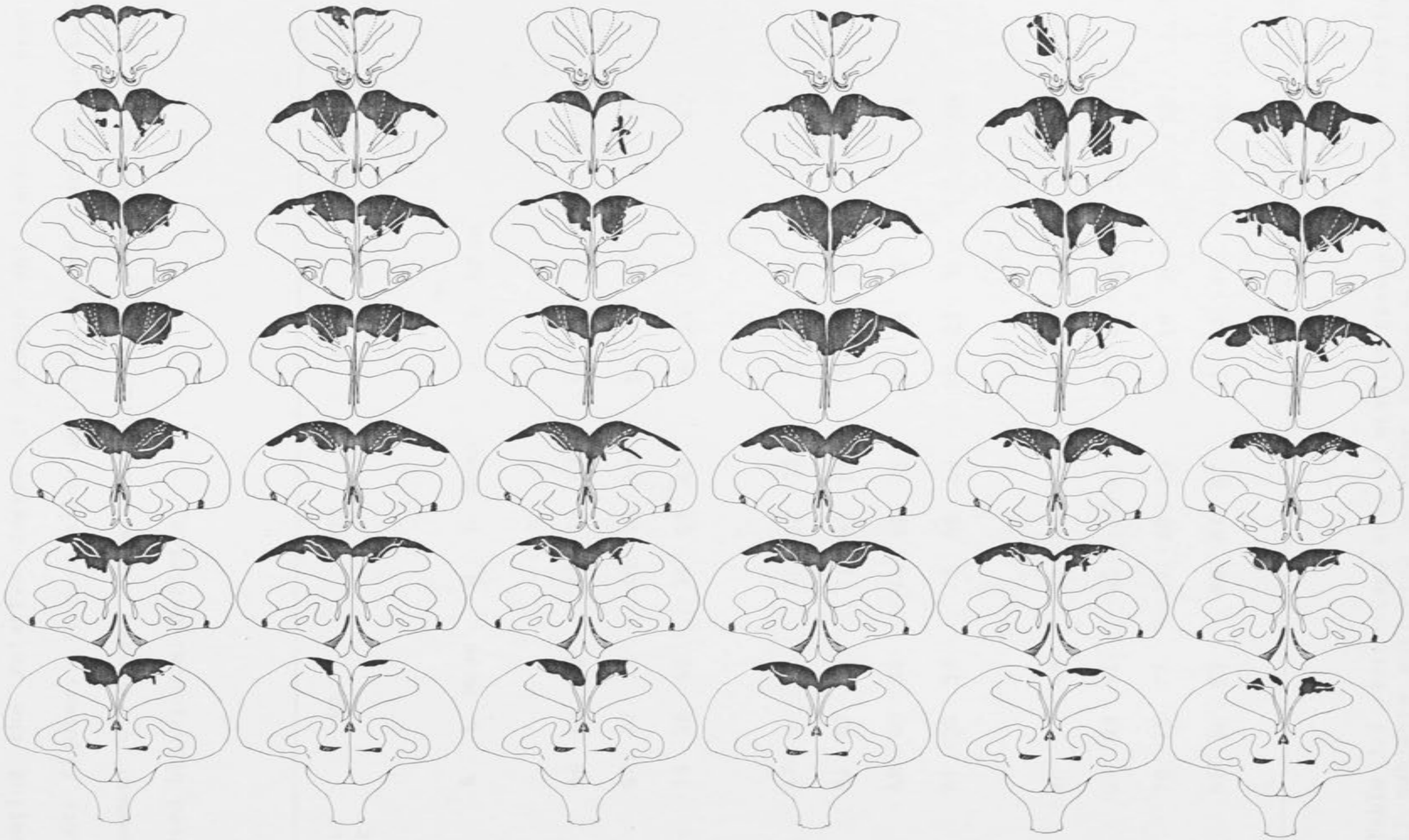
3.3.1 Anatomical

Figure 3.5 shows the reconstructions of necrosis for all Wulst lesioned subjects. The total percentage of the Wulst that was lesioned and the relative size of the lesions of the left and right major subdivisions of the hyperstriatum (HA, HIS, HD and HV) are compiled in Table 3.3. The total percentage damage to the Wulst for the sham operated controls are shown in Table 3.4. The estimates of the percentage area of damage were based upon the position of the borders of the hyperstriatum in a normal unoperated brain. The right hand side of the key shown in Figure 3.5 pictorially represents the boundaries used for each area.

The area estimates of brain damage in Tables 3.3 and 3.4 underestimate the real amount of tissue damage for a number of reasons. Firstly, upward distortions of the borders of the divisions of the hyperstriatum occurred during suction of the brain tissue. Secondly, the boundaries used to define the various subdivisions of the Wulst were taken to the extreme ventral medial border which includes the area parahippocampalis and area corticoidea dorsalateralis. In addition, not all of the Wulst has been described as receiving visual projections. For example, the anterior Wulst (see A14 in Figure 3.5) has efferent relationships which resemble the mammalian pyramidal tract (Karten *et al.*, 1973). Lesion of the anterior Wulst produced motor disorders (unpublished observations). In the present study we attempted to remove the portion of the Wulst that receives fibres from the OPT complex (known as the visual Wulst) namely, HA, HIS and HD. We attempted to spare the most anterior component (A14) and the ventral hyperstriatum (HV). The percentage

Figure 3.5 Reconstructions of the Wulst lesions for all subjects in group A. Black regions indicate necrosis. Serial sections are arranged from location A14.0 - A8.0 in steps of 1 mm according to the atlas of Karten and Hodos (1967). The subject identification numbers are indicated below each transverse series. A number of cell groups and fiber bundles including the divisions of the hyperstriatum have been identifed with abbreviations in the key. The abreviations are: BO, Bulbus olfactorius; CA, Commissura anterior; CO, Chiasma opticum; E, Ectostriatum; HA, Hyperstriatum accessorium; HD, Hyperstriatum dorsale; HIS, Hyperstriatum intercalatus superior; HV, Hyperstriatum ventrale; LPO, Lobus parolfactorius; N, Neostriatum; PA, Paleostriatum augmentatum; PP, Paleostriatum primitivum; TSM, Tractus septomesencephalicus.


A14
A13
A12
A11
A10
A9
A8
HIS
HD
HA
HV
BO
N
E
PA
LPO
TSM
PP
CA
CO
KEY
28
29
30
32
33



36 38 41 42 43 44

figures presented in Tables 3.3 and 3.4 are based upon total Wulst area including the anterior Wulst. Thus they only provide a means of estimating the relative degree of damage and cannot be read as absolute figures. It does allow us to measure the correlation between the amount of damage to a particular region of the Wulst and the observed behavioural deficits.

Subject Number	HA			HIS			HD			Total Wulst	HV
	R	L	Mean	R	L	Mean	R	L	Mean		
28	56	65	61	61	72	67	38	33	36	56	10
29	69	77	73	50	46	48	30	19	25	58	6
30	39	58	49	34	59	47	16	14	15	47	4
41	57	66	62	38	32	35	9	15	12	47	3
42	84	87	86	71	83	77	58	42	50	77	11
43	48	60	54	74	67	71	36	28	32	52	5
44	61	53	57	72	66	69	38	23	31	50	7
32	40	55	48	38	66	52	29	22	26	42	5
33	89	93	91	63	100	81	21	49	35	69	14
36	79	75	77	87	60	73	52	19	36	62	7
38	61	66	63	86	87	87	51	44	47	66	6

Table 3.3 Percentage area of missing tissue and severe cell loss for all subjects subjected to Wulst lesion surgery. Figures are to the nearest percent. HA, hyperstriatum accessorium; HIS, hyperstriatum intercalatus suprema; HD, hyperstriatum dorsal; HV, hyperstriatum ventrale; R, right hemisphere; L, left hemisphere.

Subject Number	Mean % damage to Wulst		
	Right	Left	Total
17	1.0	0.7	1.0
19	0.4	0.4	0.4
24	1.0	2.0	1.0
15	3.0	5.0	4.0
16	4.0	28.0	16.0
18	0.0	0.3	0.2
20	11.0	18.0	14.0

Table 3.4 Percentage area of damage, defined as missing tissue and severe cell loss, for all subjects that had undergone sham operations. Figures are to the nearest percent.

3.3.2 Behavioural

3.3.2.1 *Depth Acquisition (Group 1)*

All subjects learnt the SDT to criterion except subject 43, whose training was interrupted due to experimental fault. Acquisition curves for individual birds are shown in Figure 3.6. The line of best fit was calculated for each subject and the slope (SL), correlation coefficient (r) and the number of sessions (SN) taken to reach criterion are set out in Table 3.5. The correlation coefficients indicate that a linear function is a reasonable approximation of the learning curve.

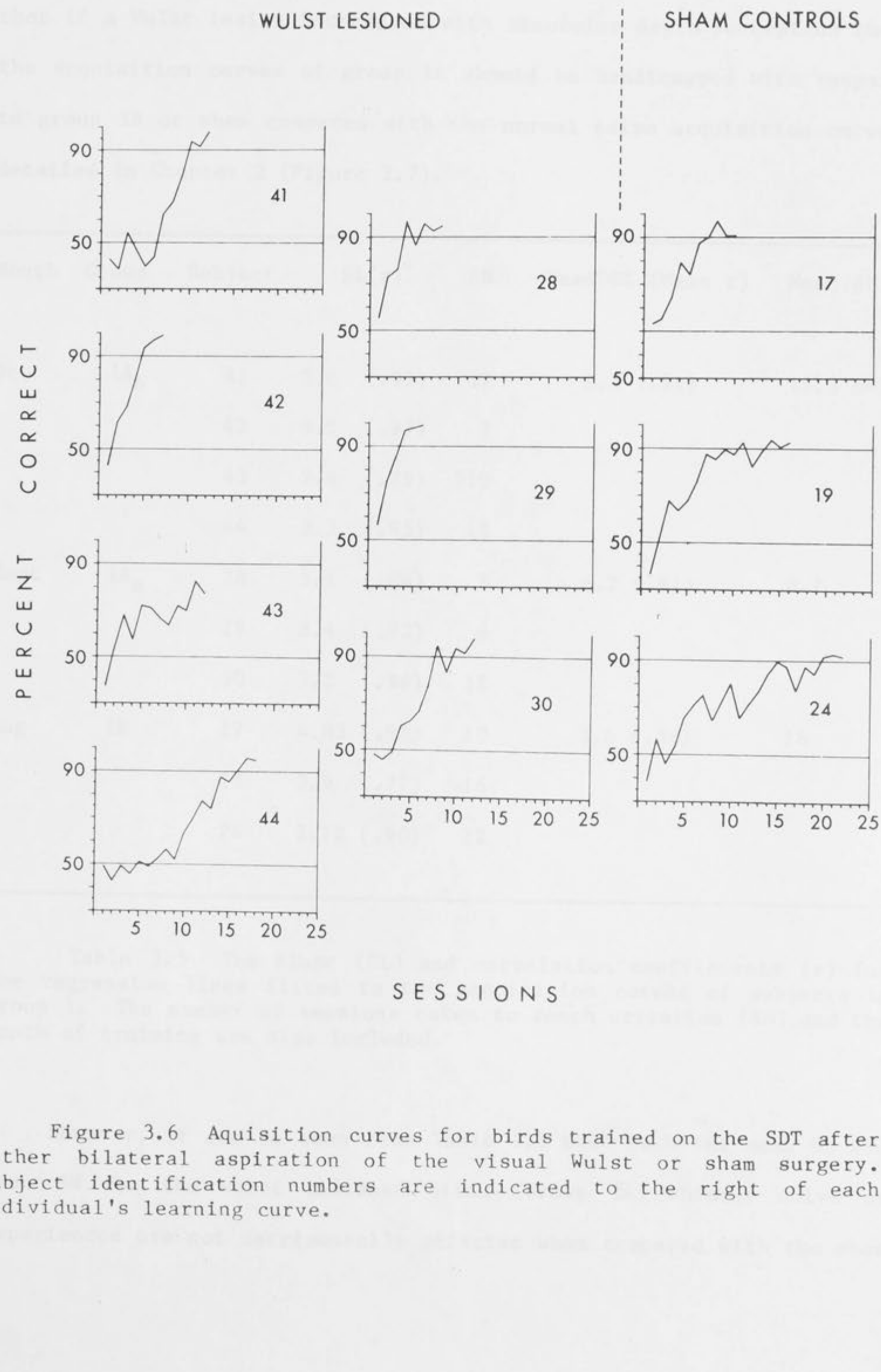


Figure 3.6 Aquisition curves for birds trained on the SDT after either bilateral aspiration of the visual Wulst or sham surgery. Subject identification numbers are indicated to the right of each individual's learning curve.

Both the mean SN and SL for the sham controls (Group 1B) fall into the normal range found in Chapter 2 for naive subjects trained on the SDT during the month of August (cf. Table 3.5 and Table 2.3). This indicates that the sham controls behave as subjects that have had no preliminary surgery or anaesthetic experience. One would expect that if a Wulst lesion interfered with binocular depth perception then the acquisition curves of group 1A should be handicapped with respect to group 1B or when compared with the normal naive acquisition curves detailed in Chapter 2 (Figure 2.7).

Month	Group	Subject	SL(r)	SN	Mean SL (Mean r)	Mean SN
Oct	$1A_n$	41	5.6 (.91)	12	5.3 (.91)	12.3 n=3
		42	9.5 (.97)	7		
		43	2.6 (.79)	>10		
		44	3.3 (.95)	18		
Sept	$1A_e$	28	5.1 (.84)	8	6.2 (.91)	8.7
		29	8.4 (.92)	6		
		30	5.2 (.96)	12		
Aug	1B	17	4.83 (.92)	10	3.6 (.86)	16
		19	3.9 (.77)	16		
		24	2.12 (.90)	22		

Table 3.5 The slope (SL) and correlation coefficients (r) for the regression lines fitted to the acquisition curves of subjects in Group 1. The number of sessions taken to reach criterion (SN) and the month of training are also included.

However, it can be seen from Table 3.5 that both the mean SL and mean SN for the Wulst lesioned birds (Group 1A) whether naive or experienced are not detrimentally affected when compared with the sham

subjects in Group 1B. When the month of training was taken into consideration and Group 1A was compared with normal acquisition (Table 2.3) it was clear that there was no difference between the mean SN and SL for Wulst lesioned birds (mean SN = 12.3, mean SL = 5.3) when compared with normal birds (mean SN = 12.8, mean SL = 4.3). The subjects of Group 1B show surprisingly fast learning curves (mean SN = 8.7, mean SL = 6.2) compared with normal birds trained in the same month (mean SN = 14.5, mean SL = 4.2). The learning rate was increased by a factor of 1.6. This effect was probably due to the experience gained by Group $1A_e$ subjects on a different discrimination task prior to being tested for acquisition of the SDT.

For Wulst lesioned birds in Group 1, the cell loss in HA and HIS was always greater than that seen in HD. Subjects 28, 42, 43 and 44 had the greatest lesion to HD which was only accompanied by slight damage to HV for subjects 28 and 42. There was no correlation between the size of the lesion to HA, HIS or HD with either SL or SN for group 1A (HA/SL r = .01; HA/SN r = -.60; HIS/SL r = .08; HIS/SN r = -.05; HD/SL r = -.05; HD/SL r = .31; HD/SN r = -.30). This becomes clear if one examines the learning curve for subject 42 (Figure 3.6). This subject had the most complete visual Wulst lesion with sparing of the anterior Wulst and little damage to HV. Yet this bird also had the fastest acquisition curve for group $1A_n$. Thus it is unlikely that lesions of the visual Wulst retard acquisition of the binocular depth task.

3.3.2.2 *Depth and Pattern Retention (Groups 2 and 3)*

The individual pre- and post-operative performances curves for subjects in groups 2 and 3 are shown in Figures 3.7 and 3.8 respectively. In each graph, mean percent correct has been plotted as a function of the number of sessions.

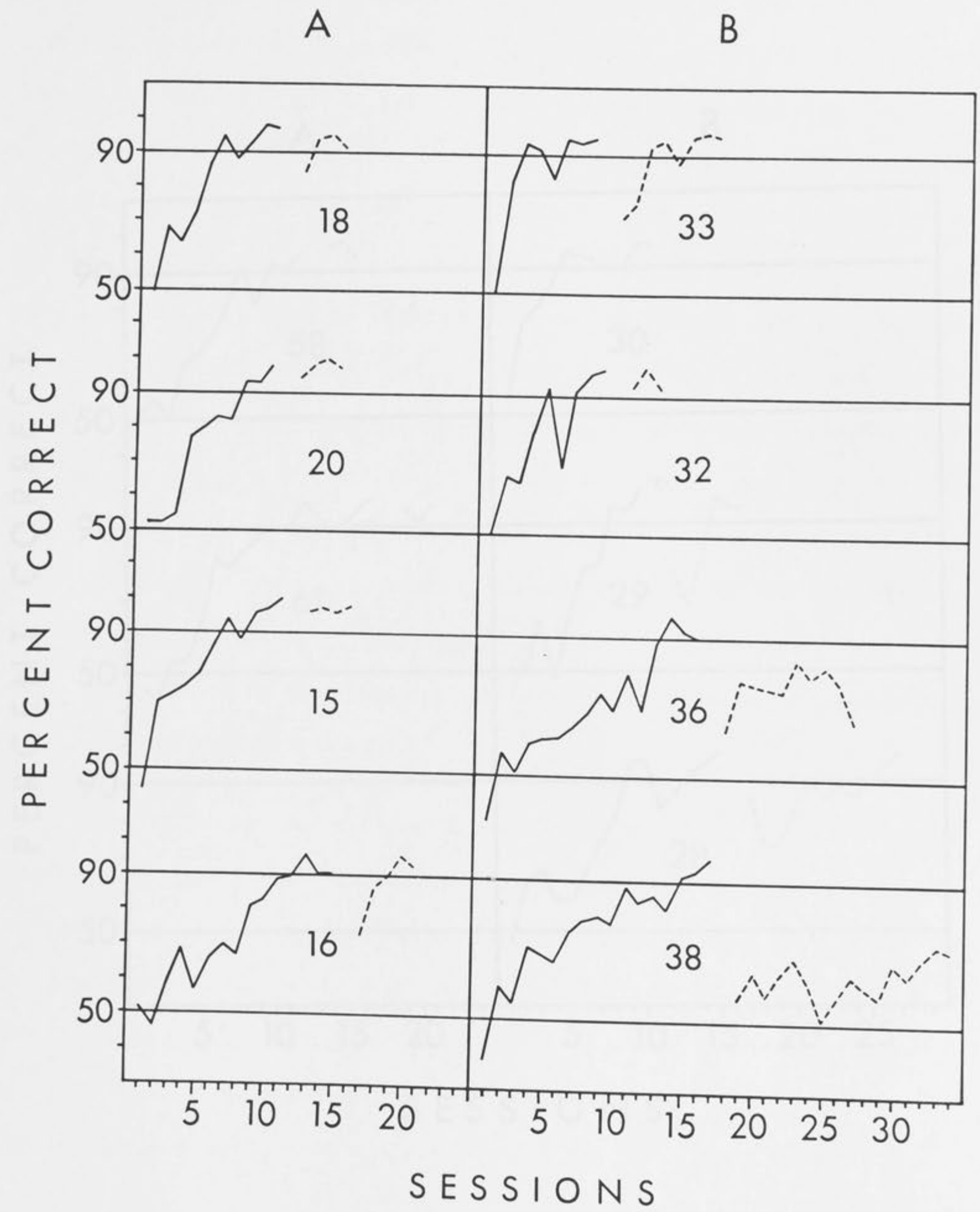


Figure 3.7 Pre-operative (solid line) and post-operative (broken line) curves for subjects trained on the SDT and tested for retention after either a sham operation (A) or a bilateral Wulst lesion (B). Subject identification numbers indicated on each graph.

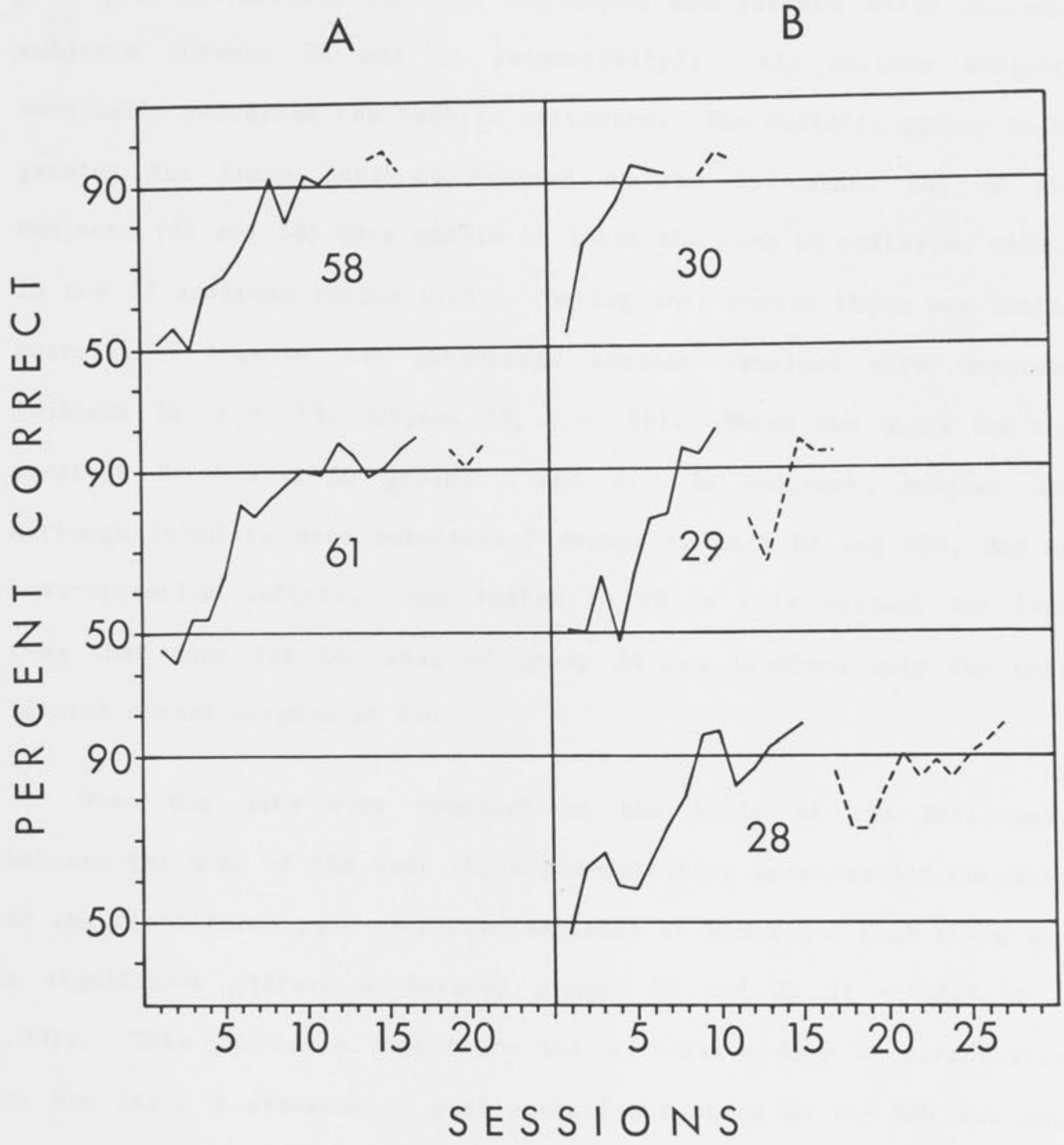


Figure 3.8 Pre-operative (solid line) and post-operative (broken line) curves for subjects trained on the Pattern 2 discrimination and tested for retention after either no surgery (A) or a bilateral Wulst lesion (B). Subject identification numbers indicated on each graph.

Subjects in the sham operated and control subgroups (2B and 3B) showed no change in performance post-operatively and remained at criterion levels of responding. In contrast, varying deficits were seen post-operatively in both the depth and pattern Wulst lesioned subjects (Groups 2A and 3A respectively). All pattern subjects eventually relearned the task to criterion. The deficits appear to be greater for those subjects trained on the SDT since two of the subjects (36 and 38) were unable to learn the task to criterion within 10 and 17 sessions respectively. During this period there was little correlation between the percentage correct obtained with sessions (subject 36, $r = .15$; subject 38, $r = .59$). These two birds had the greatest HD lesion in groups 2 and 3. In contrast, subject 32, although found to have substantial damage to both HA and HIS, had no post-operative deficit. The lesion to HD in this subject was less than that seen for the rest of group 3A and involved only the most lateral dorsal margins of HD.

When the data were compared on the basis of the difference between the mean of the last three pre-operative sessions and the mean of the first three post-operative sessions it was found that there was a significant difference between groups 2A and 2B ($t = 52.7$, $p < .001$). This indicates that there was a relative drop in performance on the first 3 sessions of post-operative testing on the SDT for the Wulst lesioned birds that was not seen in the sham operated controls.

Independently, one can also compare the pre and post-operative performance difference for the Wulst lesioned subjects trained on the SDT (group 2A) and those trained on the pattern task (group 3A). Here we find no significant difference between the two groups ($t = .07^{ns}$). For group 3A, the subject with the greatest lesion to the Wulst and HD (28) also had the longest post-operative learning

curve, while the subject with no post-operative deficit (30) had the least Wulst damage and in particular, very little damage to HD.

It would seem that for both the pattern discrimination and the SDT, behavioural deficits occurred after lesion of the Wulst, particularly if the lesion included regions of HD. This deficit was more pronounced for those subjects tested on the SDT. It is unlikely that the differential deficit was a function of the difference between the difficulty of the two tasks as there was little difference between the number of sessions to criterion pre-operatively (see Table 3.6). Thus, unlike acquisition, lesions of the visual Wulst do effect retention of the binocular depth task.

Discrimination Task	Subject	SN	Mean SN (σ)
	28	15	
	29	10	
Pattern 2	30	7	12.2 (4.0)
(group 3)	61	17	
	58	12	
	32	9	
SDT	33	8	12.5 (4.7)
(group 2A)	36	16	
	38	17	

Table 3.6 The number of sessions taken to reach criterion (SN) on the two discrimination tasks, Pattern 2 and the Standard Depth Task.

3.3.2.3 *Binocular Depth Thresholds (Group 4)*

Estimates of the retinal disparity corresponding to the smallest depth difference discernable at threshold were calculated by two methods. The absolute value of the depth threshold, in terms of retinal disparity, obtained by either method 1 or 2, depends upon the distance from the nodal point of the eye to the front face of the stimulus (d). In the following results, d was taken as equal to 89mm (see Section 3.2.6.3(iii)).

Method 1: A daily threshold was calculated from the point where the psychometric function crossed the 75% correct line (PSE). The development of the depth threshold over sessions for both the Wulst lesioned (group 4A) and normal (group 4B) birds is plotted in Figures 3.9 and 3.10 respectively. The last three disparity values plotted constitute the three successive sessions satisfying criterion. Two subjects (39 and 33) stabilised at greater than 20 minutes of arc and hence were required to achieve a second stabilisation criterion (see Section 3.2.6.3(iv)). This was obtained only for subject 39 and is indicated in Figure 3.10 by the second graph (39(ii)). The mean retinal disparity of the last three (or five for subject 39(ii)) sessions was taken as the threshold.

Method 2: Instead of calculating the threshold from the mean of individual depth thresholds, it was also possible to calculate the threshold from a single mean psychometric function. Figure 3.11 shows the mean psychometric function for each single criterion subject over the last three stable sessions. The data were plotted in terms of the mean percentage correct obtained for each depth difference (converted to retinal disparity) tested. Hence each point was a mean of 72 trials. The PSE was found where the mean psychometric function crossed the 75% correct dashed line. The corresponding retinal disparity was taken as a particular subject's threshold.

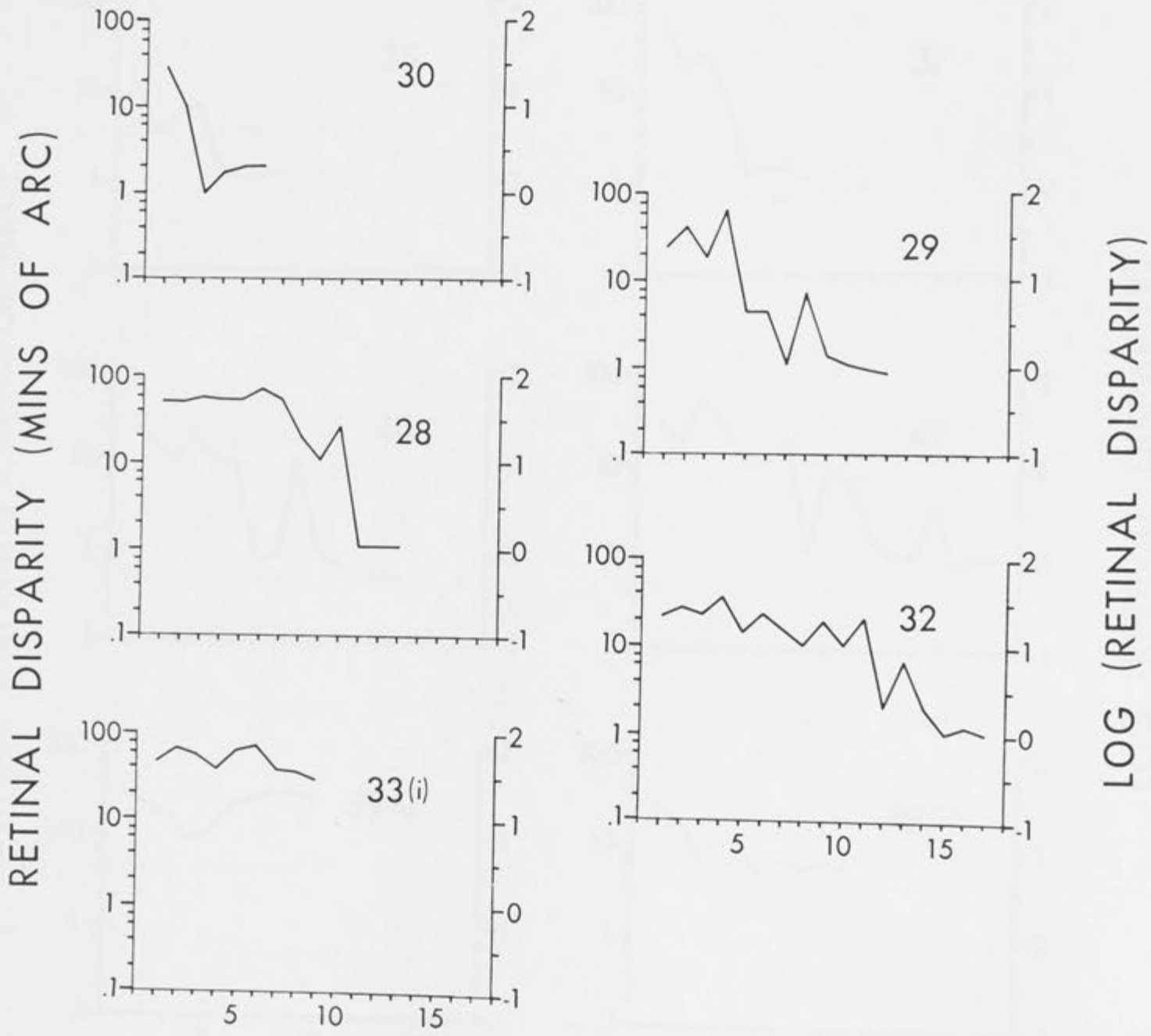


Figure 3.9 Depth thresholds, in terms of retinal disparity as a function of the number of sessions, for the cases with lesions of the Wulst. The last three disparity values plotted constitute the three successive sessions satisfying criterion, the mean of which was taken as the threshold.

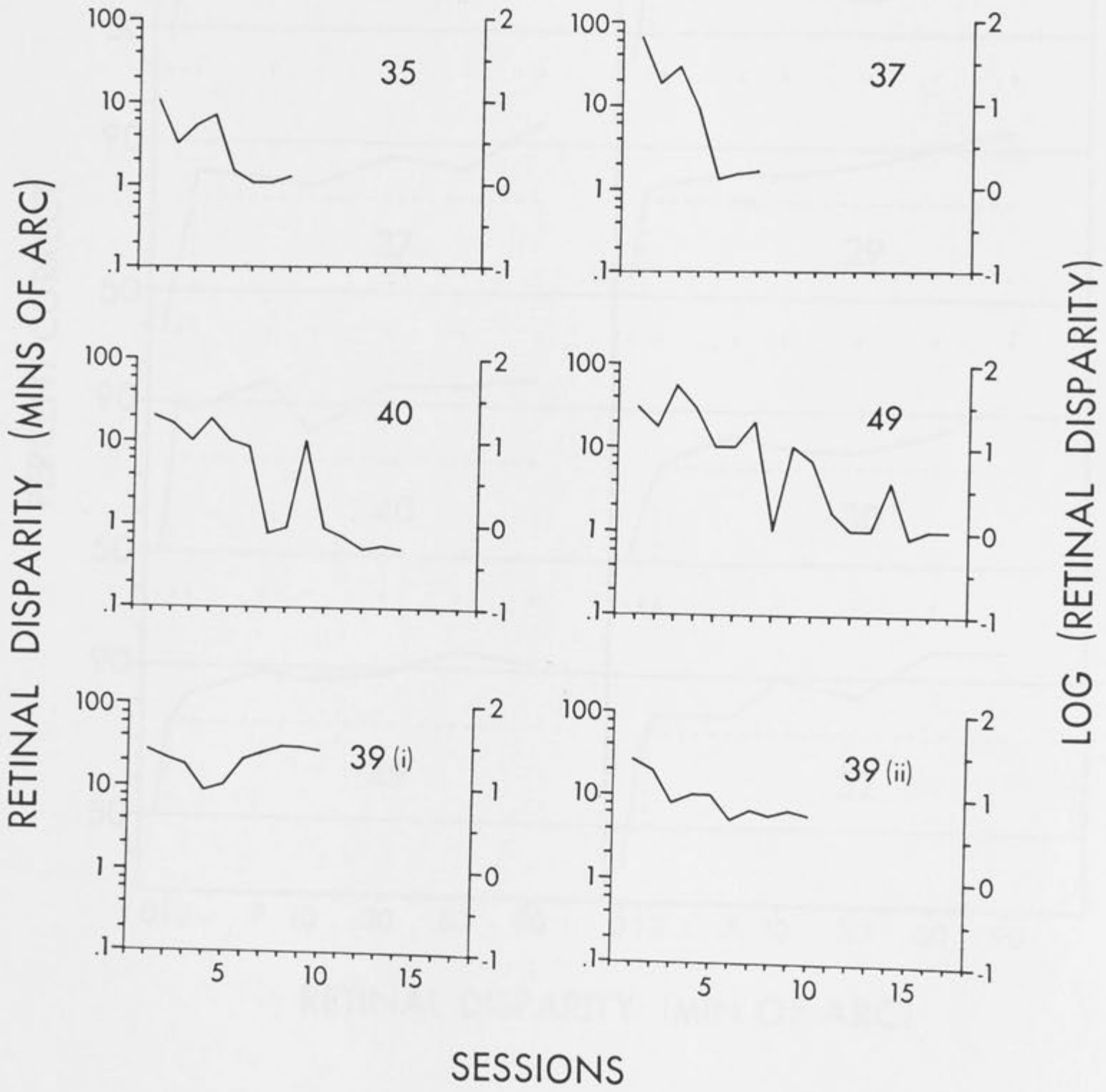


Figure 3.10 Depth thresholds, in terms of retinal disparity as a function of the number of sessions, for all normal birds tested. The last three disparity values plotted constitute criterion, the mean of which was taken as the depth threshold. Subject 39 was required to pass a second criterion (see text).

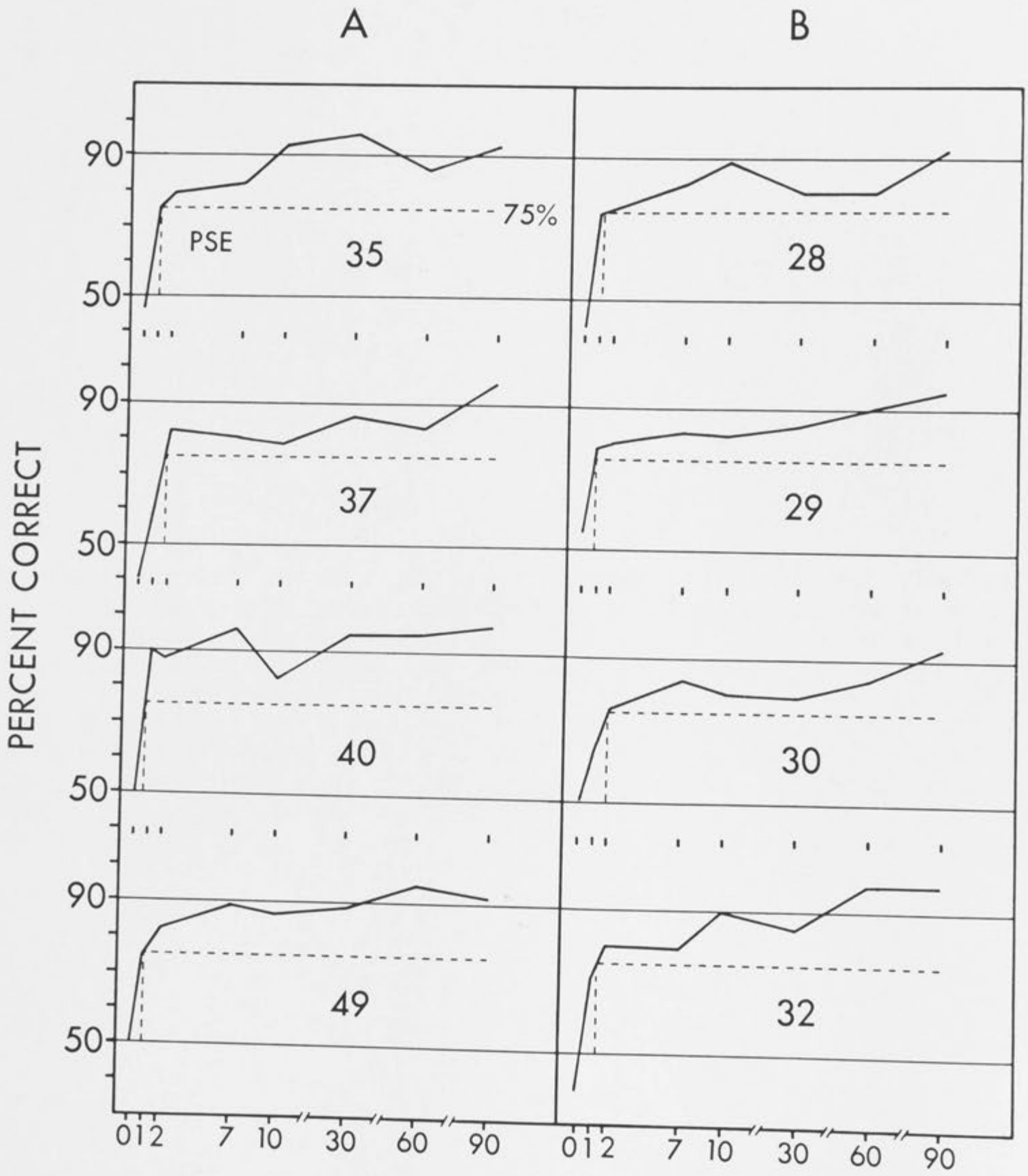


Figure 3.11 Psychometric functions for normal (A) and Wulst lesioned (B) birds based on the mean performance during the last three (stable) sessions. The horizontal broken line represents the 75% correct. The intersection of the 75% correct line with the psychometric function indicates the point of subjective equality (PSE). The corresponding retinal disparity to the PSE was taken as a particular subject's threshold.

Table 3.7 The mean threshold (γ_t) in terms of retinal disparity in mins of arc calculated for both Wulst lesioned and normal subjects by both methods 1 and 2 (see text for explanation of methods, Section 3.3.2.3). Bold lettering indicates the mean value for the data immediately above. Threshold estimates were extrapolated for those subjects indicated with an asterisk(*). IO/2, half the interocular separation; % range, percentage range of individual thresholds from the mean threshold during the last three stability sessions; SN, number of sessions of psychophysical testing required to reach criterion stability.

GROUP	SUBJECT	IO/2 (mm)	METHOD 1		METHOD 2	SN
			γ_t	% Range	γ_t	
	28	12.5	1.07	(0, 0, 0)	1.07	13
WULST	*29	12.5	.96	(12, 0, 12)	.90	12
LESIONED	30	11.5	1.87	(10, 5, 5)	1.88	6
4A	32	12.0	1.10	(6, 12, 6)	1.34	17
			1.25		**1.30**	
	33 (i)	11.75	34.86	(11, 5, 15)		9
	35	12.0	1.10	(6, 6, 12)	1.03	8
NORMAL	37	11.5	1.46	(13, 1, 11)	1.60	7
4B	*40	12.0	.73	(3, 6, 3)	.77	14
	49	12.0	.96	(15, 7, 7)	.98	17
			1.06		**1.10**	
	39 (i)	12.0	29.20	(3, 3, 6)		10
	(ii)		6.20	(15, 12, 3, 12, 5)		

Two of the pigeons (numbers 40 and 29) performed at better than 75% correct on all stimulus pairs except when the depth difference was zero. For this stimulus pair performance was 43% and 55% respectively. In order to determine a threshold for these two subjects, the daily psychometric functions (method 1) or the mean psychometric function (method 2) were extrapolated to 50% for a depth difference equal to zero (or retinal disparity equal to zero).

The mean thresholds for all subjects, in terms of retinal disparity in minutes of arc, calculated by both methods 1 and 2, are shown in Table 3.7. Also included are the percentage range about the mean of the three criterion values, the total number of sessions required to reach threshold stabilization and the interocular separation for each subject. It can be seen from Table 3.7 that one subject from each group (39, 33) stabilised at greater than 20 minutes of arc. When subject 39 was forced to complete a second stabilisation, the threshold fell to 6.2 mins of arc. A similar stabilisation was not obtained for subject 33 due to experimental interruption. Both of these subjects seem to deviate from the main group, and presumably represent a population of subjects with poorer stereoacuity than maximal or average. Excluding the deviant subjects, the mean threshold retinal disparity calculated from the depth differences for methods 1 and 2 was 1.0 and 1.1 minutes of arc for normal subjects and 1.25 and 1.3 minutes of arc for Wulst lesioned subjects respectively. Notice that method 2 gives a slightly higher estimate of the depth threshold. There was no significance difference between the normal and Wulst lesioned subjects thresholds whether calculated by method 1 ($t = .86^{ns}$, $df = 6$) or method 2 ($t = .74^{ns}$, $df = 6$). It was also found that the mean number of sessions required to achieve the first criterion did not differ between the two groups ($t = .08^{ns}$, $df = 8$).

All of the above data was based upon a viewing distance d, of 89mm. In Section 3.2.6.3(iii), it was stated that this value was most likely to give the most accurate determination of retinal disparity. However, it was also noted that the decision to peck the response key may have been made further back from the key at a maximum d of 102mm. The threshold retinal disparity calculated by method 1 was re-determined for each subject based on this extended viewing distance. The resultant range of threshold based upon the maximum and minimum viewing distances (102mm and 89mm respectively) are shown in Table 3.8. Again, there was no significant difference between the Wulst lesioned and normal subjects' thresholds based upon the maximum d_2 ($t = .86^{ns}$, $df = 6$).

The above results show that the threshold retinal disparity corresponding to the smallest depth difference discriminable is not significantly effected by partial damage to components of the hyperstriatum. It is possible that more complete lesions may have resulted in behavioural deficits. However, if the visual Wulst contributes to the behaviour in question, it is suprising that there is no noticeable effect of the lesions on such a sophisticated test as measured by a psychophysical threshold.

The absolute value of the threshold itself is of interest. It was found to be between 0.8 and 1.3 mins of arc. This depth acuity surpasses the best estimates of visual acuity measured in the pigeon to date.

Group	Subject		γ_t (mins of arc) d_1	d_2	Mean γ_t
	28		1.07	.82	
Wulst	29		.96	.73	
Lesioned	30		1.87	1.43	
	32		1.10	.83	
		Mean	**1.25**	**.95**	**1.1**
		S.D.	.42	.32	
	35		1.10	.83	
Normal	37		1.46	1.10	
	40		.73	.60	
	49		.96	.73	
		Mean	**1.06**	**.82**	**.92**
		S.D.	.31	.21	
				Grand Mean	1.0

Table 3.8 Range of thresholds (γ_t) calculated by Method 1 for each single criterion subject in the two groups 4A and 4B. The two thresholds given for each subject were based upon the maximum (d_2) and minimum (d_1) estimates of the distance d from the anterior nodal point of the eye to the front face of the stimulus; d_1 = 89mm, d_2 = 102mm; S.D., standard deviation.

3.3.2.4 *Monocular Depth Threshold (Subject 37)*

The retinal disparity corresponding to the D10 stimulus (S+ in the SDT) was approximately 200 mins of arc. Despite the large depth

difference, it was shown in Section 2.3.2.1 that all subjects (except number 37) were unable to learn to discriminate this depth difference with one eye covered. Subject 37 did learn to use available monocular cues, and it was of interest to compare the monocular and binocular thresholds for this bird. The resultant development of the depth thresholds under binocular and monocular conditions are shown in Figure 3.12. The retinal disparity threshold corresponding to the smallest depth difference discriminable calculated by Method 1 was found to be 13.2 mins of arc under monocular viewing conditions. The binocular threshold had previously been found to be between 1.1 and 1.46 mins of arc (see Table 3.8). Thus, binocular depth acuity was about ten times better than monocular depth acuity on the SDT.

3.3.2.5 *Human depth thresholds*

The psychometric function obtained for each human subject is shown in Figure 3.13. The mean retinal disparity threshold was 4.2 secs of arc. When tested with one eye occluded on a depth difference corresponding to a retinal disparity of 20 sec of arc, all subjects' performance fell to chance levels of responding ($\bar{x}$ = 52%, σ_{n-1} = 6.5%).

The experienced one-eyed subject was unable to see the displaced circle in the depth stimuli. Her response curve generated from discrimination performance on a range of retinal disparities (25-300 secs of arc) is shown in Figure 3.14. The mean percentage correct obtained was 44.8% (σ_{n-1} = 13.9%). This subject was unable to discriminate even large depth differences that were seventy times greater than the mean threshold for normal binocular subjects. A monocular threshold was unattainable.

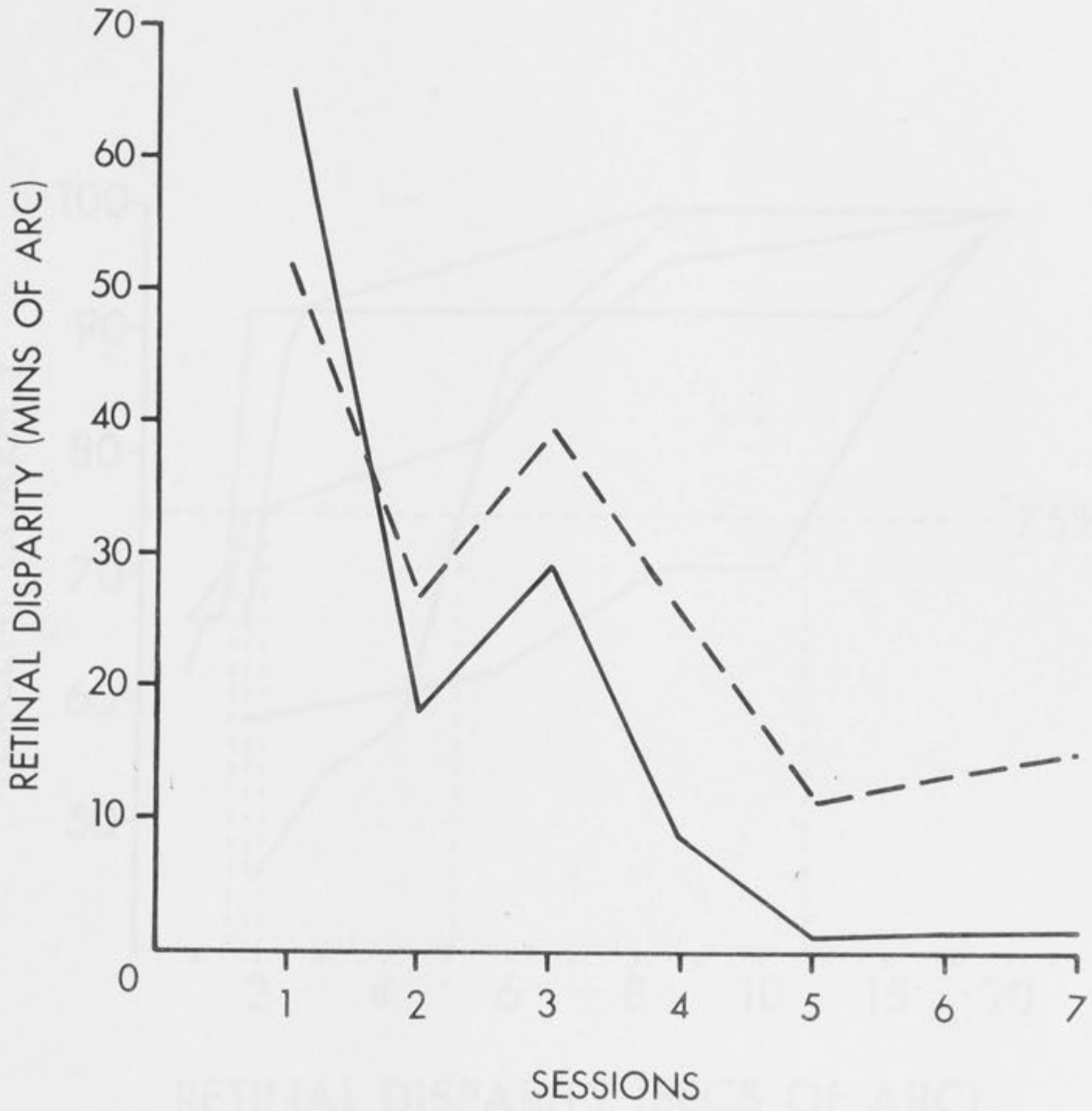


Figure 3.12 The development of binocular (solid line) and monocular (broken line) depth thresholds in terms of retinal disparity as a function of sessions for subject 37. The last three sessions constitute criterion, the mean of which was taken as the threshold.

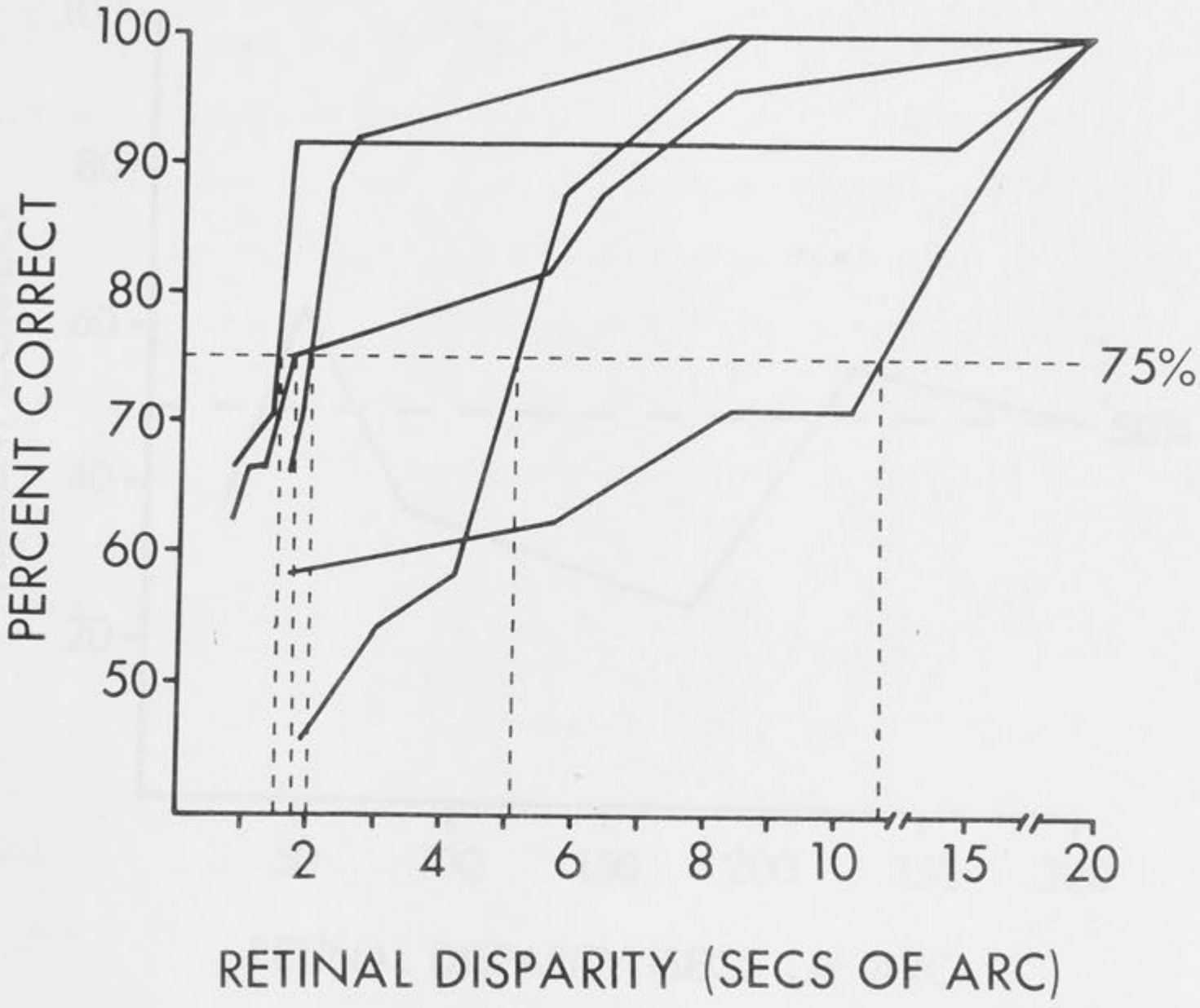


Figure 3.13 Psychometric functions within the range of 1 - 20 sec of arc for five human subjects. Performance for all subjects on depth differences greater than 20 secs of arc remained at 100% correct. The retinal disparity corresponding to the intersection of the 75% correct broken line with each individuals psychometric function was taken as the threshold.

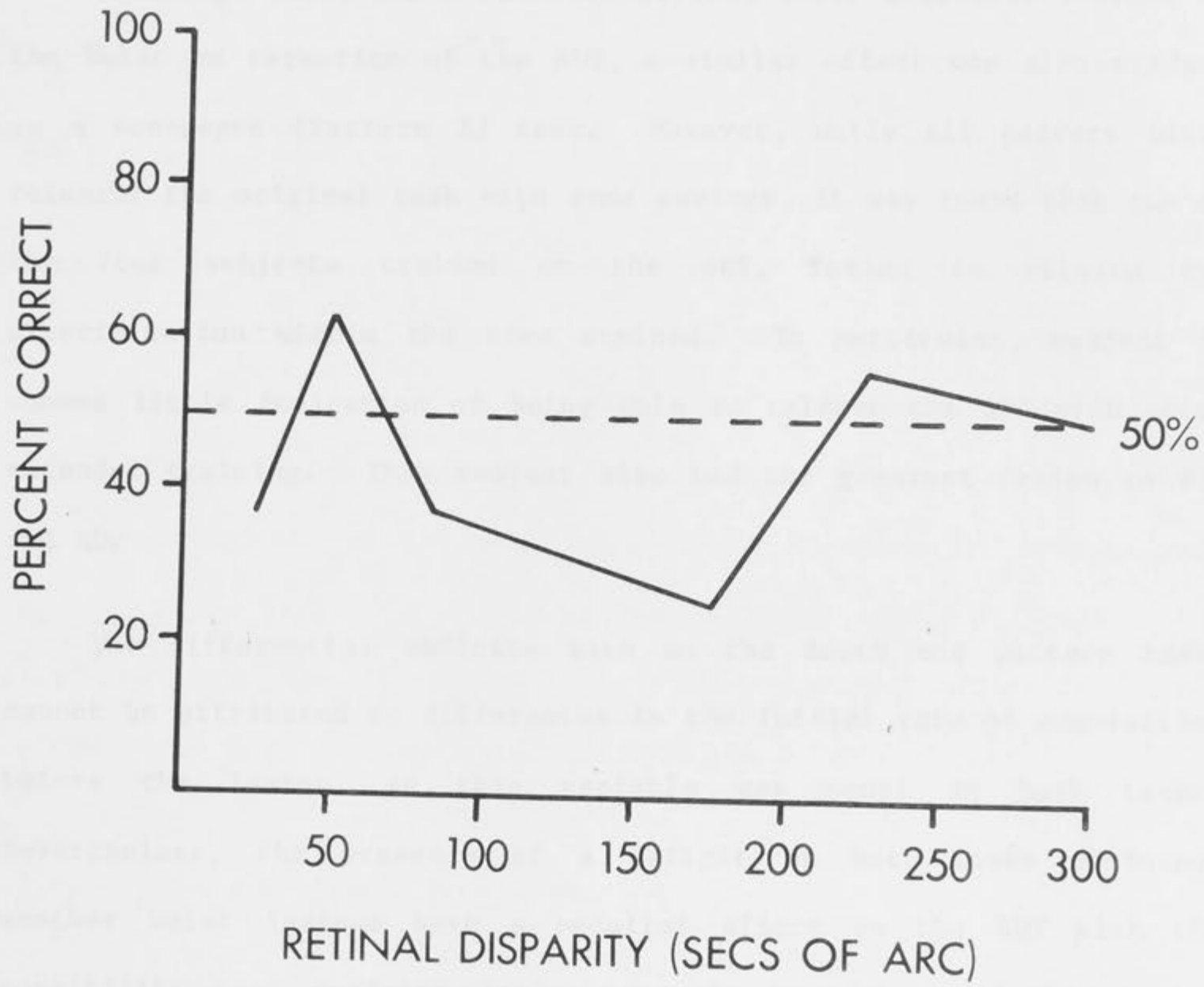


Figure 3.14 Performance curves generated by a monocular human subject on a series of depth differences over the range 50 - 300 secs of arc. Performance remained at chance levels of responding (50%) for all values tested.

3.4 DISCUSSION

3.4.1 The effect of bilateral lesions of the visual Wuslt on three behavioural measures of performance on the Standard Depth Task.

3.4.1.1 *Retention*

Although there was a moderate deficit after bilateral lesions of the Wulst on retention of the SDT, a similar effect was also evident on a non-depth (Pattern 2) task. However, while all pattern birds relearnt the original task with some savings, it was found that two of the four subjects trained on the SDT, failed to relearn the discrimination within the time trained. In particular, subject 38 showed little indication of being able to relearn the SDT even after extended training. This subject also had the greatest lesion to HIS and HD.

The differential deficits seen on the depth and pattern tasks cannot be attributed to differences in the initial rate of acquisition before the lesion, as this variable was equal in both tasks. Nevertheless, the presence of a deficit on both tasks confounds whether Wulst lesions have a peculiar affect on the SDT with the possibility that deficits are a general phenomenon associated with retention processes.

3.4.1.2 *Acquisition*

The deficits seen on retention of the SDT after Wulst ablations could be a general phenomenon associated with memory processes, since no deficits were evident on the initial acquisition of the SDT after Wulst lesions or the rate of attainment of psychophysical depth thresholds, when compared with sham or normal birds. Since it was difficult to remove the Wulst in its entirety, it is possible that

residual tissue was capable of mediating the discriminations. However, the psychophysical depth threshold measure was a sensitive test and should allow detection of subtle changes in binocular depth capabilities.

3.4.1.3 *Depth Thresholds*

No detrimental effect of partial damage to components of the hyperstriatum (HA, HIS, HD) were seen on the absolute value of the depth threshold attained. The experimental birds acquired the stabilisation criterion within the same number of sessions as normal birds, and the depth threshold as measured in various ways, did not differ significantly between the two groups. It is possible that behavioural deficits would be seen if the lesions had been more complete. In particular, it is possible that greater damage to HD may have resulted in behavioural deficits. However, it appears that damage to HA and HIS did not produce behavioural deficits. The absolute value of the smallest depth difference discriminable is also of interest in itself, and will be examined in Section 3.4.3.

3.4.2 The visual Wulst in perspective

The differential effect of Wulst lesions seen between retention and acquisition of a visual discrimination should perhaps suggest that further studies examining the role of the 'visual' Wulst, should not only look at retention, as is the normal procedure, but also the acquisition of the particular task under study. The results of this study contradict those of Zeigler (1963) who found that the primary effect of hyperstriatal lesions was on the process of acquisition rather than retention. The contradiction appears less pronounced when one compares the lesions in each case. Subjects in Zeigler's study had destruction that included HV. This non-Wulst area of the

hyperstriatum received none or very little damage in the present study.

The minor effects of Wulst lesions on the SDT reported here are perhaps not surprising when one recalls that lesions in all parts of the thalamofugal system, particularly the Wulst, have surprisingly little effect on a range of visual discriminations (Hodos *et al.*, 1973; Pritz, Mead and Northcutt, 1970). Only sophisticated psychophysical testing methods reveal lesion effects (Pasternak and Hodos, 1977), but performance still subsequently returns to pre-operative levels. In contrast lesions in various components of the tectofugal system can produce severe impairment of visual discriminations (Cohen, 1967a; Hodos and Karten, 1966, 1970, 1974) including the acquisition of intensity and pattern tasks (Hodos and Fletcher, 1974).

The results of this study show that components of the 'visual' Wulst do not independently mediate binocular depth perception in the pigeon. On this point it is interesting to note that in the rhesus monkey, global stereopsis is left quite intact after complete destruction of those portions of areas VI or V2 concerned with central vision. Yet these are the areas where local disparity is reported to be coded (Hubel and Wiesel, 1970; Poggio and Fisher, 1977; Cowey and Porter, 1979).

The existence of parallel anatomical pathways and the demonstration of both excitatory and inhibitory interactions between these pathways (see for example with respect to the avian brain: Holden, 1968; Bagnoli *et al.*, 1979) have important implications for the interpretation of behavioural changes following visual system lesions (see Hodos *et al.*, 1982). The role of a cell group which alone does not mediate a particular visual test, may be to modulate

the activity of another cell group in a parallel pathway in order for the visual system as a whole to function properly. Because of the numerous opportunities for parallel interactions within the visual system, one can easily be misled by interpreting lesion effects solely within the context of serial pathways.

Neurophysiological studies have demonstrated substrates for local disparity detectors in the Wulst of the frontally-eyed owl and the falcon (Pettigrew and Konishi, 1976a; Pettigrew, 1979). However, the pattern of bilateral label after thalamic injections of HRP in the pigeon is quite different from that described in the falcon (Lehmkuhle *et al.*, 1977). Indeed, after Wulst injections of HRP, no ectostriatal label has been found in this species either . In the owl too, there is no clear evidence for which OPT thalamic nuclei correspond to those described in the pigeon (Karten *et al.*, 1973) making cytoarchitectural comparisons difficult. Although there are striking similarities across different species in the organisation of the visual pathway, Adamo (1967) in examining connections of the avian forebrain in different species stresses that:

> assumed generalizations concerning data obtained from avian forms should take into consideration the fact that species differences can and do exist...

Finally, it should be noted that electrophysiological recordings in the Wulst of the pigeon have found two distinct retinotopically organized maps of visual space, one lying subjacent to the other in HA. Although a large proportion of the map was devoted to that part of the visual field immediately in front of the beak, only a very few binocular cells were encountered (Frost *et al.*, 1983). This result is in line with the results of the present study.

3.4.3 The binocular depth acuity of the pigeon

In examining the depth acuity of the pigeon, it was found that there were two distinct populations. The majority of birds fell into a group which obtained a mean threshold of approximately one minute of arc. However, 20% of the sample proved to have a very poor depth acuity in comparison to the other birds.

The two deviant subjects (numbers 33 and 39) stabilised at some 20 times the normal threshold. After further training and a stricter criterion, one subject was induced to improve its depth threshold, but it was still five times greater than the mean threshold found for the larger population of subjects. Just as one would expect some subjects to have poorer acuity than optimum, these two subjects presumably represent a population with poor stereoacuity. (The reason why I refer to the psychophysical depth threshold as indicative of stereoacuity will become clear in Section 3.4.3.2). Indeed, stereoblindness is a common phenomenon affecting the human population. Richards (1970, 1971) has described three classes or disparity detectors in man: crossed, mean zero and uncrossed disparity. He found that the probability of lacking one of these detector classes was as high as 30% (see also Jones, 1977; Blake, 1982). More peripheral factors affecting eye alignment will also clearly interfere with the normal convergence necessary for binocular single vision.

The remaining pigeons were found to have a mean threshold in terms of retinal disparity between 0.8 and 1.3 mins of arc depending on the method of calculation. It will be shown in Section 3.4.3.1 that such a high depth acuity is superior to the normal visual acuity of the pigeon as measured by numerous methods.

3.4.3.1 *Comparison of the binocular depth acuity with other forms of visual acuity.*

The range of free-viewing acuity threshold values calculated for the pigeon vary considerably (1.5 - 5 mins of arc) and depend in part on whether the stimuli are distant (Chard, 1938; Blough, 1971; Uhlrich *et al.*, 1982) or near (Nye, 1968; Blough, 1973; Hodos *et al.*, 1976; Hodos and Leibowitz, 1977). There is accumulating evidence to suggest that the pigeon is inherently myopic in its anterior binocular field and hypermetropic in the lateral visual field (Catania, 1964; Millodot and Blough, 1971; Nye, 1973). Bloch and Martinoya (1982) compared the frontal and lateral visual acuity of the pigeon as a function of viewing distance. In agreement with the suggestion of Catania (1963) they found that frontal acuity decreases with distance while lateral acuity increases with viewing distance. For viewing distances of 10cm, close to the distances used by the birds in obtaining the SDT threshold reported here (see Section 3.2.6.3(iii)), the frontal acuity was 3.5 times better than the corresponding lateral acuity. However, the actual threshold values reported in this study were very poor. Thus, the minimum acuity threshold for frontal viewing at 10cm was 8 mins of arc, while the corresponding lateral acuity was only 30 mins of arc. These high values were probably due to the tachistoscopic nature of test stimuli which severely reduces viewing time. The lowest thresholds for the pigeon reported to date, are by Hodos *et al.* (1976) and Nye (1968). All other free-viewing estimates are of the order of 3-5 mins of arc, some four times the depth acuity reported in this thesis.

Acuity measurements depend on a number of factors, not the least of which is the luminance of the stimulus. Hodos *et al.* (1976) measured the visual acuity with diagonal high-contrast gratings as a function of stimulus luminance. Grating acuity improved with

increasing luminance and was highest at a luminance of 2.3 cd/m^2 after which acuity deteriorated. This luminance corresponds to the luminance level used in the present study in measuring depth thresholds (see Section 2.2.2). Hodos found that optimum resolution involved the detection of an angle of 1.9 mins of arc.

The absolute size of the stimulus is also a variable to be considered. Nye (1968) employed a significantly larger grating pattern (58^o) than Hodos *et al.* (1976) and obtained the binocular near field acuity of the unrestrained pigeon in terms of the Modulation Transfer Function (MTF). He estimates the peak sensitivity to be at a spatial frequency of .07 cycles/min. arc. It is difficult to specify an upper limit of spatial resolution from the MTFs due to the negatively accelerated slope at high frequencies. Donovan (1978) suggsts that a conservative estimate might be a minimum separable angle of 1.5 minutes, while Hodos *et al.* (1976) extrapolates Nye's functions to 100% contrast and obtains a visual acuity estimate of 1.3 minutes at a luminance of .56 cd/m^2. Nye's unusually high estimate of acuity is due in part to his criteria (60%) for determining the PSE. Lower thresholds would have resulted had he used the more conventional 75% criterion used by other authors.

All the estimates of acuity reported above do not meet the depth acuity reported in this study. Here, the mean retinal disparity corresponding to the smallest depth difference detectable at threshold for all non-deviant subjects was about 1 min of arc. Hence the pigeons' acuity for resolving depth differences surpasses the highest estimates of spatial frequency acuity (Nye, 1968) and is better than the optimum resolution of gratings (Hodos *et al.*, 1976) at a similar luminance level by a factor of 1.5 - 2.

Nye (1968) estimates the minimum intercone spacing in the pigeon retina uncorrected for shrinkage to be 1.54 minutes. This figure would be increased by approximately 10% if shrinkage was also considered. Given a similar figure for the feral pigeons used in this thesis, would mean that their depth acuity is finer than the sampling mosaic of the retina. Furthermore, the density of the ganglion cell mosaic and associated size distribution of receptor field centers reflects the degree of convergence from receptors to ganglion cells with a concomitant loss in spatial information. When these factors are considered, together with possible non optimum optics due to eye movements, it is clear that the depth acuity reported here is possibly within the realms of hyperacuity.

3.4.3.2 *Hyperacuity*

In the human visual system, the phenomenon of hyperacuity has been known since 1892, when Wuelfig (see Berry, 1948) measured vernier thresholds. Westheimer (1975) coined the term and much literature has been concerned with how such acuities transcend the resolution limitation of physiological optics (see Hecht and Mintz, 1939; Westheimer, 1975; Braddick, 1984).

Of all the hyperacuities, stereoscopic acuity has access to the smallest distinctions between local signs. A direct comparison of human vernier, stereoscopic (using a haploscopic device) and real depth acuities by Berry (1948) revealed that there was no appreciable difference between real and stereoscopic depth thresholds and they were of the order of 2-4 seconds of arc. This agrees with the mean human threshold value for the depth discrimination reported in this chapter (see Section 3.3.2.5) which was found to be 4 seconds of arc. Thus, there is little doubt that the human thresholds on the SDT reflect stereoacuity. Indeed, monocular human subjects were unable to

attain a similar threshold and one adult subject who only had vision in one eye since an early age was unable to discriminate a depth difference as great as 300 seconds of arc.

Although there are several important similarities between the factors affecting stereoacuity and either vernier acuity of spatial interval discrimination (Butler and Westheimer, 1978; Westheimer and McKee, 1978; Westheimer, 1979), it is unlikely that depth discrimination could be interpreted as merely the combination of vernier discrimination of each eye alone (Berry *et al.*, 1950; Stigmar, 1970; Westheimer and McKee, 1979). Whatever the human mechanism(s) for stereoacuity, the superior performance of the pigeons' depth acuity when compared with its binocular visual acuity, clearly cannot be attributed simply to binocular summation (Campbell and Green, 1965).

Since the pigeons' binocular depth threshold reported in the results of this chapter is better than their spatial frequency acuity and appears to be a hyperacuity, it is possible that the depth acuity is based upon stereopsis. The depth mechanism is clearly highly tuned to small differences in the position of objects in space and is binocularly based. Thus, unless one wishes to postulate new binocular mechanisms underlying the perception of depth apart from those traditionally described, stereopsis remains a likely candidate. Further evidence that binocular vision is required to achieve a depth threshold in terms of retinal disparity of about 1 minute of arc, was found when threshold performance under monocular conditions was examined.

3.4.3.3 *Monocular threshold performance on the SDT*

Most subjects were unable to discriminate very large depth differences with one eye covered. Only one subject was able to learn to use subtle monocular cues to discriminate small differences in depth in the Frisby stimuli. After prolonged training it was found that this subject attained a monocular threshold ten times larger than its corresponding binocular threshold. Thus, the superior binocular performance found in chapter 2 was also evident at threshold levels.

3.4.4 Open Questions

Given that the pigeon does possess binocular depth perception with an acuity that implies it may be stereopsis, it remains to be seen where this information is primarily processed. Chapter 4 in this thesis will address this issue.

CHAPTER FOUR

THE ROLE OF THE INTERHEMISHPERIC CONNECTIONS IN THE BINOCULAR PERCEPTION OF DEPTH

CONTENTS

4.1 INTRODUCTION

It has been shown that performance on a depth discrimination using stimuli with strong retinal disparity cues, was superior under binocular rather than monocular viewing conditions. These results support the hypothesis that the pigeon utilizes binocular cue(s) for the near perception of depth. Furthermore, the binocular mechanism, whatever its form, mediates excellent depth acuity for near vision. The question arises as to where the neural binocular interaction occurs. Clear evidence was presented that the 'visual' Wulst was not necessary for the adequate functioning of the binocular depth mechanism. However, it is possible that this structure may modulate other structures operating in a serial hierarchy, or be one of the substations in a network of parallel processing.

A different approach to finding out which visual system pathway(s) and/or structures are involved in the integration of binocular information is to take advantage of the peculiar nature of the avian visual system. Since the optic nerve fibres are exclusively distributed to the contralateral side of the brain (Cowan *et al.*, 1961; Polyak, 1957; Karten and Nauta, 1968; Streit *et al.*, 1980) a partial decussation must occur at some subsequent stage in the visual system. Identification of the pathways critical for the transfer of monocular visual information can thus be theoretically achieved by selective and progressive interruptions to different interhemispheric connections

4.1.1 The Interhemispheric Connections

4.1.1.1 *Supraoptic Decussation (DSO)*

Fibres recrossing through the ventral aspect of the supraoptic decussation (DSO_v) merge with the crossed fibres in the nucleus rotundus (Rt) of the retinotectal system (Benowitz and Karten, 1976; Hunt and Kunzle, 1976; Reperant *et al.*, 1977). Fibres also cross the midline through the dorsal aspect of the supraoptic decussation (DSO_d) and project to the hyperstriatum intercalatus superior (IHA), the telencephalic target area of retino-thalamic afferents (Karten and Nauta, 1968; Perisic *et al.*, 1971; Hunt and Webster, 1972; Karten *et al.*, 1973; Meier *et al.*, 1974; Mihailovic *et al.*, 1974). DSO also takes crossed fibres from the tectum to nucleus subpretectalis (SP), nucleus interstitio-pretecto-subpretectalis (IPS), and nucleus triangularis (T) (Karten, 1965; Karten and Revzin, 1966; Meier *et al.*, 1974, Benowitz and Karten, 1976; Hunt and Kunzle, 1976; Reperant *et al.*, 1977).

It is reported that tectal fibres which enter the ipsilateral brachium of the superior colliculus (BCS) also cross the midline via the DSO to end in the nucleus posteroventralis thalami (PV) and the ventral lateral geniculate nucleus (GLv) (Voneida and Mello, 1975) the latter itself a recipient of primary retinal input (Cowan *et al.*, 1961; Karten and Nauta, 1968; Meier *et al.*, 1974).

4.1.1.2 *Tectal Commissure (CT)*

Fibres of the tecto-tectal projection exit the ipsilateral stratum album centrale and cross the midline via the CT to the deep layers of the opposite tectum (Robert and Cuenod, 1969; Barth and Felix, 1974; Hunt and Kunzle, 1976; Reperant *et al.*, 1977). Terminations are found in the contralateral stratum album centrale and

stratum periventriculare and the periventricular cells immediately under the ventricle (Voneida and Mello, 1975).

4.1.1.3 *Posterior Commissure (CP)*

Tectal fibres also cross the midline via the CP to terminate in the area pretectalis (AP), nucleus of Darkshevitch (D) and the nucleus interstitialis of Cajal (IS) (Voneida and Mello, 1975; Streit *et al.*, 1980).

4.1.1.4 *Tegmental Decussations*

Tectal lesions have also been reported to consistently give rise to degenerating axons which cross the midline in either the mid-tegmental region or in the ventral tegmental decussation. Fibres terminate mostly in nucleus linearis caudalis (LC) and to a lesser extent in the lateral reticular nucleus and medial longitudinal fasciculus (Voneida and Mello, 1975).

4.1.1.5 *Anterior Commissure (CA)*

The anterior commissure (CA) is an interhemispheric commissure connecting many forebrain sites. The CA has not been implicated in the visual system but is mentioned here because of its prominence and will be discussed in what follows.

Thus, the interhemispheric connections relay input from both eyes to a variety of visual nucleui.

4.1.2 Interocular Transfer (IOT) of Visual Discrimination Learning

The role of some of the above commissures has been examined in the process of interocular transfer (IOT) of visual discriminations. IOT is said to occur when criterion performance attained on a visual discrimination task, learned with only one eye, is immediately present when the subject is then tested with the untrained eye. Interocular transfer (IOT) was originally described for brightness discrimination in chicks, where pecking was the required operant response (Kohler, 1917 cited in Levine, 1945a). More recently Catania (1965) found complete IOT in pigeons of brightness, colour and pattern discriminations, even if a previously acquired discrimination response was reversed. Most investigators have found nearly perfect IOT in a wide variety of visual discrimination habits using operant conditioning and key pecking responses (Mello, 1966, 1968; Ogawa and Ohinata, 1966; Cuenod and Zeier, 1967; Cheney and Tam, 1972, Green *et al.*, 1978).

Cuenod and Zeier (1967) studied the effect of sectioning either the posterior and tectal commissures (CP and CT) or the anterior commissure (CA) on the IOT of a simultaneous two-key colour discrimination. They found that all birds were capable of positive IOT after complete section of the CA. Of the three birds with complete section of the CT and CP, two showed no evidence of IOT, and one showed perfect transfer. Of the subjects with partial damage to the CT and CP, there was a correlation with the obtained transfer scores, although full recovery took place rapidly with training. This puzzling pattern is also reported to have occurred in a pattern discrimination using a go, no-go training procedure (see Stettner, 1974, p. 192). Transection of CP and CT has been reported to severely retard the IOT of autoshaping in a varible time 60 sec schedule on a

go, no-go discrimination (Essock-Vitale, 1979). However, other authors have claimed that no IOT occurs in a very similar autoshape schedule in normal birds (Stevens and Kirsch, 1980). The reason for the contradiction in results is not readily apparent. Essock-Vitale also reported that transection of CP and CT had no effect on the IOT of colour and form discriminations.

Mello (1968) found that pigeons monocularly trained on pattern and colour discriminations, still showed IOT after a unilateral lesion to the contralateral tectum of the eye trained. Although Mello interpreted these results in terms of bilateral memory traces being formed at the time of training, it is also possible that the required information was processed by the thalamofugal system and transfer occurred via DSO.

The role of the DSO was addressed in a detailed study by Meier (1971). He found little deficit on colour or mirror image pattern discriminations after CP and CT were sectioned, but severe impairment if the DSO was cut. Transection of DSO in the juvenile pigeon also completely interrupts IOT of pattern discriminations (Burkhalter and Cuenod, 1978). IOT still occurs if the DSO is cut *after* a colour discrimination has been learned monocularly (O'Connell, 1979 cited in Goodale and Graves, 1982) indicating that Mello's conclusions were correct.

There appears to be little doubt of the pronounced role of the DSO in the transfer of visual discrimination learning. In contrast, most authors report that transection of the commissures at the tectal level has little effect on the interocular transfer of visual discriminations. This implies that a bilateral memory trace for pattern vision is formed primarily at thalamic or forebrain levels of the visual system.

4.1.3 Interocular Transfer as a Function of Retinal Locus

Interocular transfer has been observed not only in key pecking tasks but also in an imprinting situation (Moltz and Stettner, 1962) and in the suppression of the innate pecking response in newly-hatched chicks caused by an aversive stimulus (Cherkin, 1970). However, there also occur numerous situations in which interocular transfer (IOT) fails to occur.

Lack of transfer has been evident in such diverse situations as adaptation to the 'deep' side of a visual cliff (Zeier, 1970), extinction of the passive avoidance habit (Benowitz, 1974), pattern discrimination in chicks pecking for a heat reward (Gaston, 1979) and sometimes imprinting (Klopfer, 1973). Using an appetitive task in which pigeons had to approach the stimuli from some distance, Beritov and Chichinadze (1936) found no evidence of IOT of either colour or pattern discriminations.

Although there appear to be multiple factors affecting interocular transfer, Levine (1945a, b; 1952) reported that position of the stimuli within the visual field was a critical determinant. Using a Lashley jumping stand, he showed that there was no IOT of brightness, colour or pattern discriminations when the stimuli were presented high in the visual field in front of the pigeon, but that there was transfer when the discrimination was presented below the pigeon's head. Levine indicated that only in the latter case were the stimuli within the binocular field.

Levine's conclusions were challenged by Catania (1965) who found complete IOT whether the stimuli were located above and in front of the bird behind the response key or if located in the lateral visual field. Subsequent work by Graves and Goodale (1977) and Goodale and

Graves (1980a, b) again found no interocular transfer using a jumping stand, thus replicating Levine's findings. They also found that the discrepancies could not be accounted for by inadequate adaptation to postural changes when the 'naive' eye was tested, or by differences in task difficulty as originally indicated by Catania (1963, 1965). Goodale and Graves (1982) propose that interocular transfer occurs as a function of retinal locus. Those tasks in which the stimuli are within the binocular field (which they ascribe as projecting to the 'red area' of the retina) will be transferred interocularly, while those stimulating other parts of the retina (e.g. lateral fields) will not. Goodale and Graves propose that transfer results from the normal mechanisms underlying binocular perception. Thus they claim that absence of IOT in certain situations is a consequence of the discriminative stimuli falling within the monocular field, where there is no necessity for later convergence of input from the two eyes.

4.1.4 The Interhemispheric Connections and the Binocular Perception of Depth

The clearly defined function of the supraoptic decussation (DSO) in the interocular transfer of visual information, and the possibility that Goodale's hypothesis is correct, would lead to the expectation that binocular depth perception may also be mediated via the DSO.

Goodale's hypothesis fails to account for the findings of Catania (1965). Catania found that interocular transfer (IOT) could occur for laterally viewed colour stimuli not within the binocular field. Furthermore, Zeier (1976, cited in Goodale & Graves, 1982) has found that pigeons showed no evidence of IOT when trained on a sequential key-pecking task in which viewing was restricted to the frontal field. Here, pigeons were monocularly trained to make one pecking

response on the left and then one on the right key. Similarly Green *et al.* (1978) found that when pigeons were trained on a task in which visual signals indicated the appropriate spatial response, they were unable to perform above chance levels during transfer tests. There is also evidence to suggest that the nature of the response requirement is a critical factor in IOT. Thus Stevens and Kirsch (1980) found that although visual discrimination transferred interocularly, motor response training did not.

Thus, it is also possible that the binocular integration of monocular visual information occurs via the commissural systems at the level of the tectum. The functional role of the intertectal connections is unknown.

Voneida and Mello (1975) suggest that the tegmental decussations may be involved in visually guided behaviour. Midline tegmental section in the cat and monkey, was found to result in severe and long-lasting deficits in responsitivity to visual cues (Voneida, 1970). The general behaviour of the tegmental-split animals resembled that seen in humans with bilateral injuries in the region of the angular gyri. Holmes and Horrox (1919) describe such a patient who was unable to estimate the relative positions of objects, either in space or with relation to himself. This patient reported that he could see objects but frequently ran into them since he could not appreciate their location or distance. Although the link here is premature, the similarities in behaviour reported by Voneida and Holmes & Horrox are striking. In attempts to obtain tegmental transected pigeons, I also found that subjects were severely impaired in their response to visual cues. Such birds would freeze in the operant chamber, had altered postural changes or adopted a continuous circling behaviour and were unsuitable for behavioural testing. Therefore, no attempt was made to

examine the role of the tegmental decussations in the binocular perception of depth.

The following studies present evidence that the tectal and posterior commissures and to a lesser extent the ventral supraoptic decussation, mediate the binocular perception of depth in the pigeon.

4.2 METHODS

4.2.1 Subjects and Design

Fourteen naive and two experienced* feral pigeons were reduced to 80% of their *ad-libitum* weight as described in Section 2.2.1. The subjects were randomly assigned to one of four tasks either under lesion or sham conditions. The assignment of subjects to groups is shown in Table 4.1. The within measures design allows for the same subject to be tested twice under a single followed by a double lesion condition. The experienced birds (numbers 37 and 48) did not have prior exposure to their particular discrimination task. Subject 37 had experience on the SDT under threshold and monocular conditions before the present experiment while subject 48 had been previously trained on the SDT.

TASK	SURGICAL CONDITIONS			
	EXPERIMENTAL		SHAM	
	L1	L3	L2	L4
	CA + DSO	CP + CT	CA	SHAM (CP+CT)
SDT	45,52,56	56		
Pattern 2	*48,58	58		
SDT-Th	47	47	40	40
LACE	*37,55,57 59,62,64	37,55 57,59	67,68	67,68

Table 4.1 Assignment of subjects to conditions. Numbers indicate identification tag of each subject. Experienced subjects indicated by * (see text for details). All subjects were subjected to section of the anterior commissure (CA). DSO, supraoptic decussation; CP + CT, posterior plus tectal commissures; SDT, standard depth task; Th, thresholds.

4.2.2 Apparatus and Stimuli

The apparatus has been described in Section 2.2.2. The stimuli used for the SDT, Pattern 2 and SDT-Thresholds (SDT-Th) have also been previously described (see Sections 2.2.3.1, 3.2.3.2, 3.2.3.3 respectively).

The stimuli used in the LACE task have not yet been described in previous chapters. They were a more sophisticated version of depth stimuli developed from the SDT stimuli. Depth was present over the entire positive stimulus giving a 'lacy' two-dimensional pattern.

The LACE task consisted of a stimulus pair in which S+ = LACE 6 and S- = CLACE 6.

CLACE 6: The control LACE task stimulus consisted of an array of random sized triangles of similar density to that used for the CLD10 (see Section 2.2.3.2) which was placed onto the front of a piece of optically clear glass 6mm thick (Figure 4.1A).

LACE 6: The LACE 6 stimulus consisted of an identical array to CLACE 6, which was divided such that alternating triangles over the entire array were displaced onto the back of a piece of optically clear glass 6mm thick. The remaining half of the array was placed onto the front of the same piece of glass (Figure 4.1B).

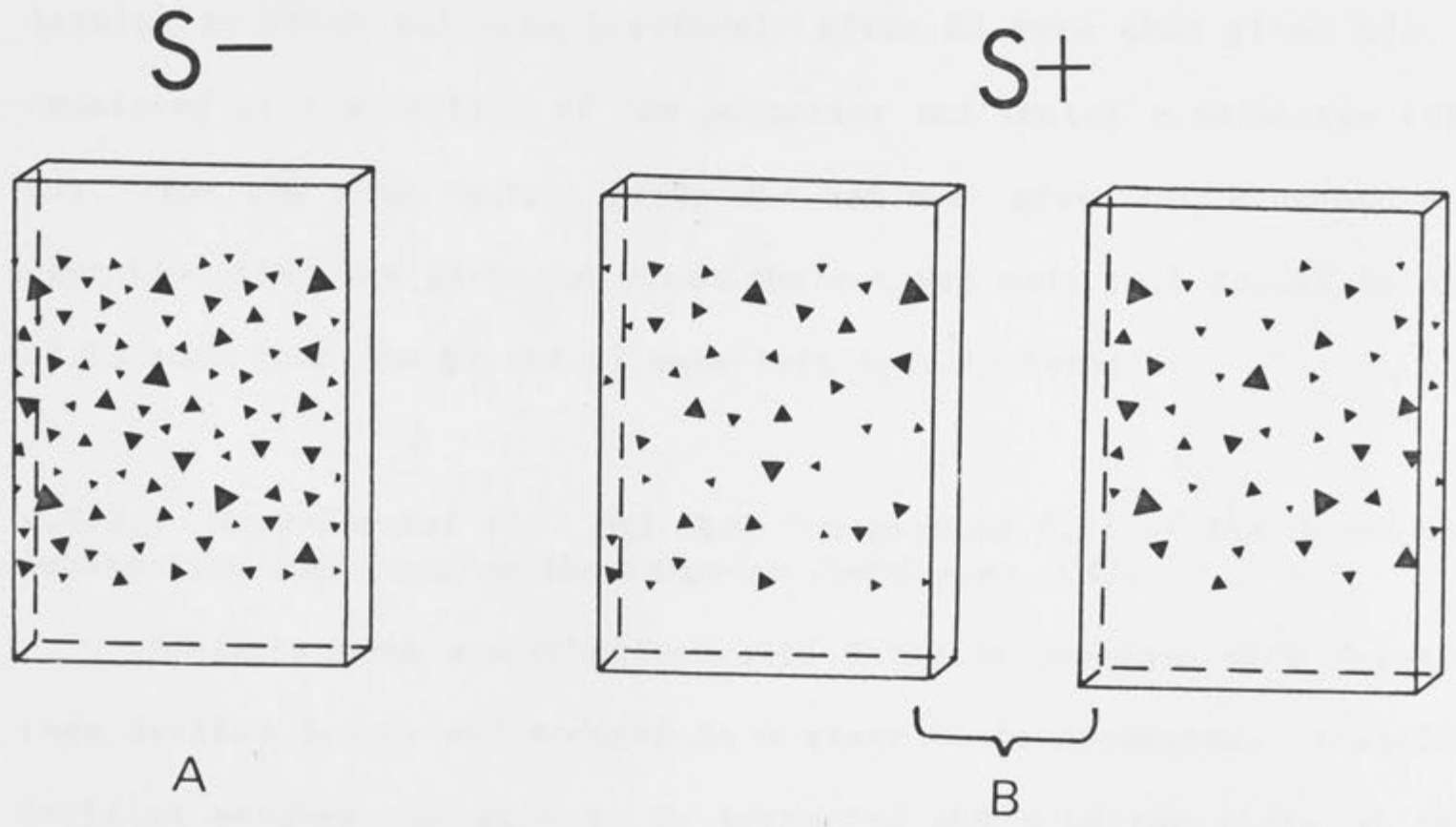


Figure 4.1 The positive (S+) and negative (S-) stimuli for the LACE task. A. The control stimulus; B. The front and back faces of the depth stimulus.

The main difference between the stimuli used in the SDT and those described above for the LACE task is that in the former an ordered global configuration (a circle) occurred as a function of the retinal disparity present. In the LACE task positive stimulus, no such intrinsic form was present. Instead, equal local disparities between adjacent elements were distributed over the entire stimulus. Thus, in terms of retinal disparity, local stereopsis produced the impression of depth.

4.2.3 Surgical Procedure

Subjects were given either single or double surgical sessions. During the first surgical session, either the supraoptic decussation (DSO) and the anterior commissure (CA) were transected (L1) *or* subjects were given a sham operation in which only the CA was cut (L2). The same birds were subsequently treated in a second surgical session in which subjects previously given L1 were then given L3. L3 consisted of transection of the posterior and tectal commissures (CP + CT). For the sham control group who had been given L2, a second sham operation (L4) was given in which the cut was made just dorsal to that of L3 such that the CP and CT were left totally intact.

4.2.3.1 *Experimental (L1) and Sham Transection (L2) of the Supraoptic Decussation (DSO) and/or the Anterior Commissure (CA).*

Subjects were anaesthetized with Ketamine combined with Xylazine (see Section 3.2.4) and secured in a stereotaxic apparatus. A midline incision enabled the skin to be retracted and a narrow plate of bone from approximately A9.0 - A5.0 and ML ± 3.0 (see Karten and Hodos, 1967) was removed taking particular care at the point overlying the midsaggital sinus at the most posterior end of the large hemispheres. The bone was kept moistened with saline. The dura was

removed from the exposed left hand side except over the sinus which was cauterized at both exposed extremes. The large left hand blood vessel feeding into the main sinus (generally placed at the back of the Wulst) was also coagulated. The hemispheres were gently parted and a size 11 sterile scalpel blade inserted with the tip at A7.5 to a depth of DV4.0 (L1) or DV3.5 (L2). The blade had been aligned with the cutting edge facing posterior and parallel to the vertical axis of the stereotaxic instrument. After insertion, the blade was moved back to A6.5 (L1 and L2) then retracted through the original path (Figure 4.2). The plate of bone was padded with a piece of gelfoam and secured in the original position with a cross of dental cement. The wound was cleaned and stiched with a silk suture.

4.2.3.2 *Experimental (L3) and Sham Transections (L4) of the Tectal plus Posterior Commissures (CT+CP).*

A similar procedure to that described above was followed during the second surgical session. After the skin was cut on the midline, the remains of the previous sutures were removed. The same plate of bone was easily removed by chipping off the dental cement and carefully levering the bone plate taking care not to pull the build-up of scar tissue. In some cases the bone had regrown and had to be re-drilled.

The exposed brain generally contained scar tissue on the midline and the left hand side. This was removed over the midline and the hemispheres gently parted. No cauterization was necessary. A sterile size 11 scalpel blade was aligned with the cutting edge facing posterior and tilted at 24° to the vertical axis of the instrument (Figure 4.2). The blade was inserted with the tip at AP0.0 to a depth of DV7.2 (L3) or DV6.5 (L4). In the case of the experimental birds, the commissures (CP + CT) were then cut by moving the blade back

2.8mm, up 2.8mm down 2.8mm and finally retracting along the original path.

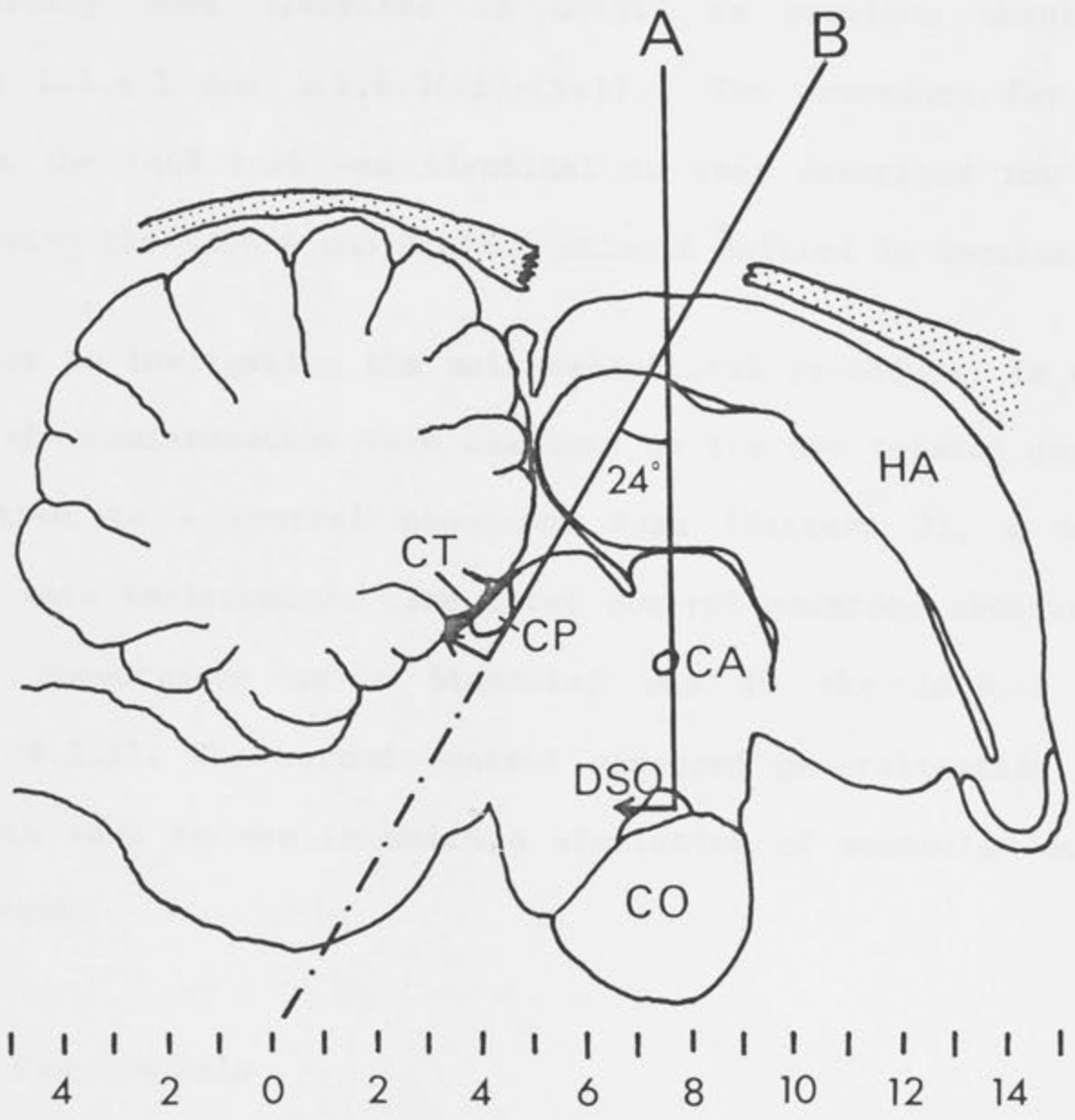


Figure 4.2 Midsaggital section showing approach for commissurotomy: A. Track for transection of DSO; B. Track for transection of CP+CT; Overlying bone indicated by striped plate; AP scale is in mm divisions; CA, anterior commissure; CO, optic chiasm; CP, posterior commissure; CT, tectal commissure; DSO, supraoptic decussation.

4.2.4 Behavioural Procedure

4.2.4.1 *Pre-Operative Training*

All subjects were trained with daily sessions (96 trials/day) to criterion or until threshold was attained (subjects 40 and 47) on their assigned discrimination as indicated in Table 4.1. The training procedures for the SDT, SDT Thresholds and Pattern 2 discriminations have already been described in detail in previous chapters (see Sections 2.2.4.2 and 3.2.6.3(ii)-(iv)). The procedure for training birds on the LACE task was identical to that described for the SDT, except using the LACE 6 and CLACE 6 stimuli defined in Section 4.2.2.

Prior to instigating the main behavioural procedure, in which the effects of commissurotomy were examined on the two related depth tasks in addition to a control non-depth task (Pattern 2), a number of controls were implemented. The first control examined absolute versus relative convergence as a binocular cue in the LACE 6 stimulus (Section 4.2.2). The second control measured generalisation from the real depth task to one in which a simulation of monocular depth cues were present.

4.2.4.2 *Cue Controls*

At the completion of criterion and prior to any surgery, subjects 55, 57 and 59 (LACE task) and 56 (SDT) were tested for one session on each of two controls. Subjects 58 and 61 (Pattern 2) were also tested on the first of these controls.

(i) *Flip Control:* The first control involved flipping both the negative (S-) and positive (S+) stimuli while maintaining the original relative position of the elements. For Pattern 2, the checkerboard patterns were presented on the back rather than on the front of the

optically clear glass. Thus the stimuli were simply further away from the subject. Flipping the stimuli in the depth tasks had a differential effect on the negative and positive stimuli. For both depth tasks, flipping S- had the effect of transposing the triangle array onto the back rather than the front of the optically clear glass. For the LACE task, S+ remained the same, with triangle arrays on both sides of the stimulus. For the SDT, S+ changed to D-10 inverted (see Section 2.2.3.3), such that the circle now appeared in front of the surround. The flip control was tested in order to see how each task withstood manipulation of the absolute and relative planes of focus. A full discussion of the implications of this control is detailed in Section 4.4.4.

(ii) *Monocular simulation:* For both the depth tasks, a second control session was undertaken with S+ changed as follows. Stimuli were made in which the random triangle arrays were only in one plane (as in S-) but distorted as if the depth stimulus was viewed from an oblique angle. Hence the new S+ simulated monocular cues to depth, such as object overlay and/or a static image produced during motion parallax, but no binocular cues were present. The new S+ for the two depth tasks are depicted in Figure 4.3.

At the completion of control testing, criterion performance was re-established on the original discrimination. In all cases, only one session was required. During subsequent behavioural training and testing, all subjects were occasionally tested on the standard control (see Section 2.2.4.2), in which S+ was changed and made equivalent to S-. At no time during this session did any subject attain scores significantly greater than chance.

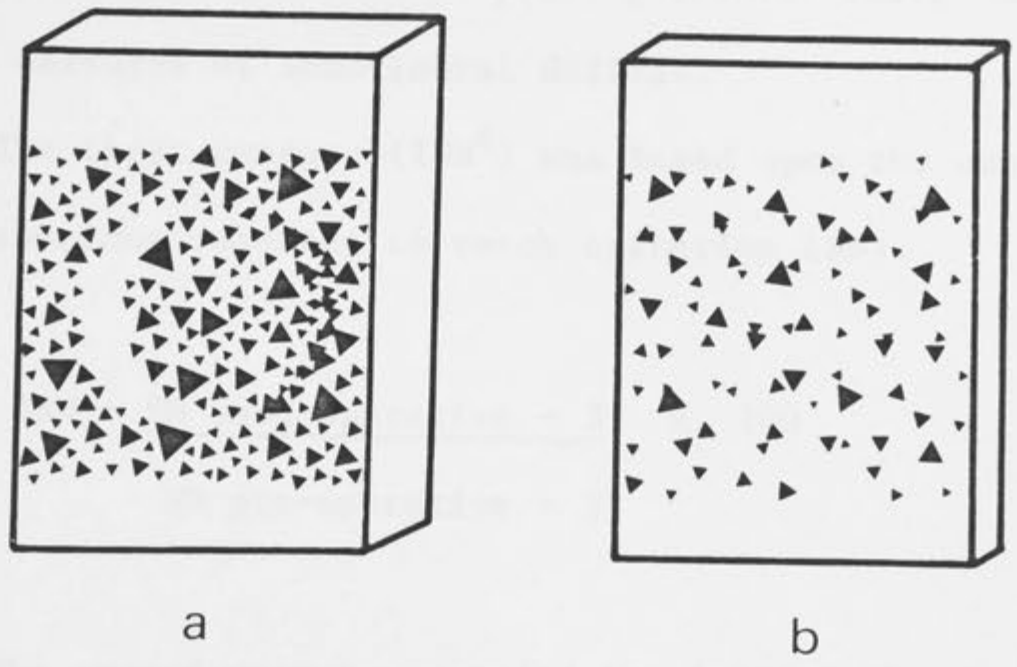


Figure 4.3 The positive stimulus (S+) used during the monocular cue simulation for; a. the SDT , b. the LACE task. The triangle arrays were only in one plane on the front of the glass stimulus.

4.2.4.3 *Post-Operative Testing*

The day following the completion of training, each subject received transection of DSO and CA (L1) or CA alone (L2). Subjects were then allowed to recover for 5-7 days before post-operative I testing on the pre-operative discrimination was undertaken. Testing was continued until criterion was re-established, or in the case of the two birds for which thresholds were measured, until four sessions were completed.

The day following the completion of post-operative I testing, each subject received transection of CP + CT (L3) or was given a sham operation (L4). Subjects were again allowed 5-7 days recovery in the home cage before post-operative II testing on the same pre-operative discrimination was undertaken[3]. Testing II was continued for a maximum of 30 sessions.

[3]The second surgical session was not successful for all subjects due to unusual sensitivity to the Pentathesin anaesthetic during the breeding season (see Section 3.2.4.2). All successful operations were done using Ketalar.

The data from each of the post-operative tests was used to calculate two measures of behavioural deficit.

(i): The first measure (%SN[4]) was based upon the number of sessions required to reach criterion (SN).

$$\%SN = \frac{\text{SN post-operative} - 3}{\text{SN pre-operative} - 3} \times 100$$

(ii): The second measure recorded the initial change (ΔC[5]) in performance on the first three post-operative sessions relative to normal pre-operative criterion performance.

ΔC = Mean of first 3 post-operative sessions
- Mean of last 3 pre-operative sessions.

4.2.5 Monocular Testing

At the completion of post-operative testing, all subjects that had been trained on a depth discrimination (SDT or LACE task) were tested on the same discrimination with one eye occluded. The method of occlusion has already been described (see Section 2.2.4.3). The eye for occlusion was chosen at random and testing was continued until monocular performance either attained criterion or stabilized for five successive sessions (15% range about the mean). Each session consisted of four monocular blocks (96 trials) and one binocular block

[4] If %SN = 0, there was no deficit and the post-operative performance remained at criterion. If %SN = 100, the subject required the same number of sessions post-operatively as pre-operatively, to reach criterion.

[5] If $\Delta C=0$, no change in performance occurred, while $\Delta C = -50$ records a maximum deficit. Small positive values of ΔC were also found, indicating small improvements in the mean percentage correct response.

(24 trials) with the order of monocular and binocular blocks randomized.

After the completion of monocular testing with either the left or right eye, further monocular testing was initiated with the opposite eye occluded. This was again continued until performance reached criterion or stabilised for five successive sessions. Hence it was possible to measure the monocular deficit present after commissurotomy or a sham operation in birds trained on the LACE task. Furthermore, by testing and training with the same eye (rather than alternating from one eye to the other) it was possible to measure the interocular transfer (IOT) to the eye untrained in using monocular cues to depth.

4.2.6 Pecking Ability after Commissurotomy

Apart from the operant procedures described above, seven subjects were also tested for their ability to accurately peck at grain. Each subject was tested prior to any surgical intervention (normal), and then after CA + DSO were cut (L1), and finally, after CP + CT were transected (L3) in the same birds. The grain was the normal feed given to maintain 80% body weight, the smallest pieces of which were also presented in the hopper of the operant box. Four sizes of grain were tested. Listed from largest to smallest they were corn, peas, millet and wheat. During each test a subject was given ten individual presentations of each sized grain by hand. Grain was placed on a mat white background in the centre of a tray (90 x 60mm). The tray was presented in the home cage.

The total number of pecks required to pick up each piece of grain was noted, and the mean number of pecks claculated for the ten presentations. Each type of grain was tested in this manner in random order. The whole procedure was repeated five times at various

intervals over a two day period. Subjects' pecking efficiency was repeatedly measured prior to any surgical treatment, and then 10-15 days after each of the commissurotomies.

4.2.7 Reconstruction of the lesions

The lesions were examined after the completion of the behavioural testing. Subjects were anaesthetized with an overdose of Pentathesin and perfused through the heart with saline followed by 10% formaldehyde-saline solution. The head was severed from the body, the calcarium removed and the brain *in situ* was submerged in a 10% formaldehyde-saline solution overnight. The head was then placed in the stereotaxic instrument and blocked in the stereotaxic plane as described by Karten and Hodos (1967). The brain was removed from the skull and placed in 20% sucrose fixative until it sank (24-48 hours).

Sections were cut at 40 μm on a freezing microtome. Every second section was mounted onto gelatinised slides to form two alternate series and dried overnight. Series A were stained with Luxol Fast Blue M.B.S. for two hours at room temperature, counterstained with Neutral Red (1%) for thirty mins, dehydrated and cleaned in eucalyptus oil according to the method of Disbrey and Rack (1970). Series B were treated with 5% celloidin in ethyl alcohol and then silver stained according to Holmes Method for nerve fibres (see Dyke, 1947).

At the completion of staining all slides were coverslipped and examined with the light microscope for evidence of cell and fibre damage. The extent of the knife track, degenerating axons and missing fibres were mapped and appropriate sections were photographed with the aid of a Photomakroskop (Wild M400).

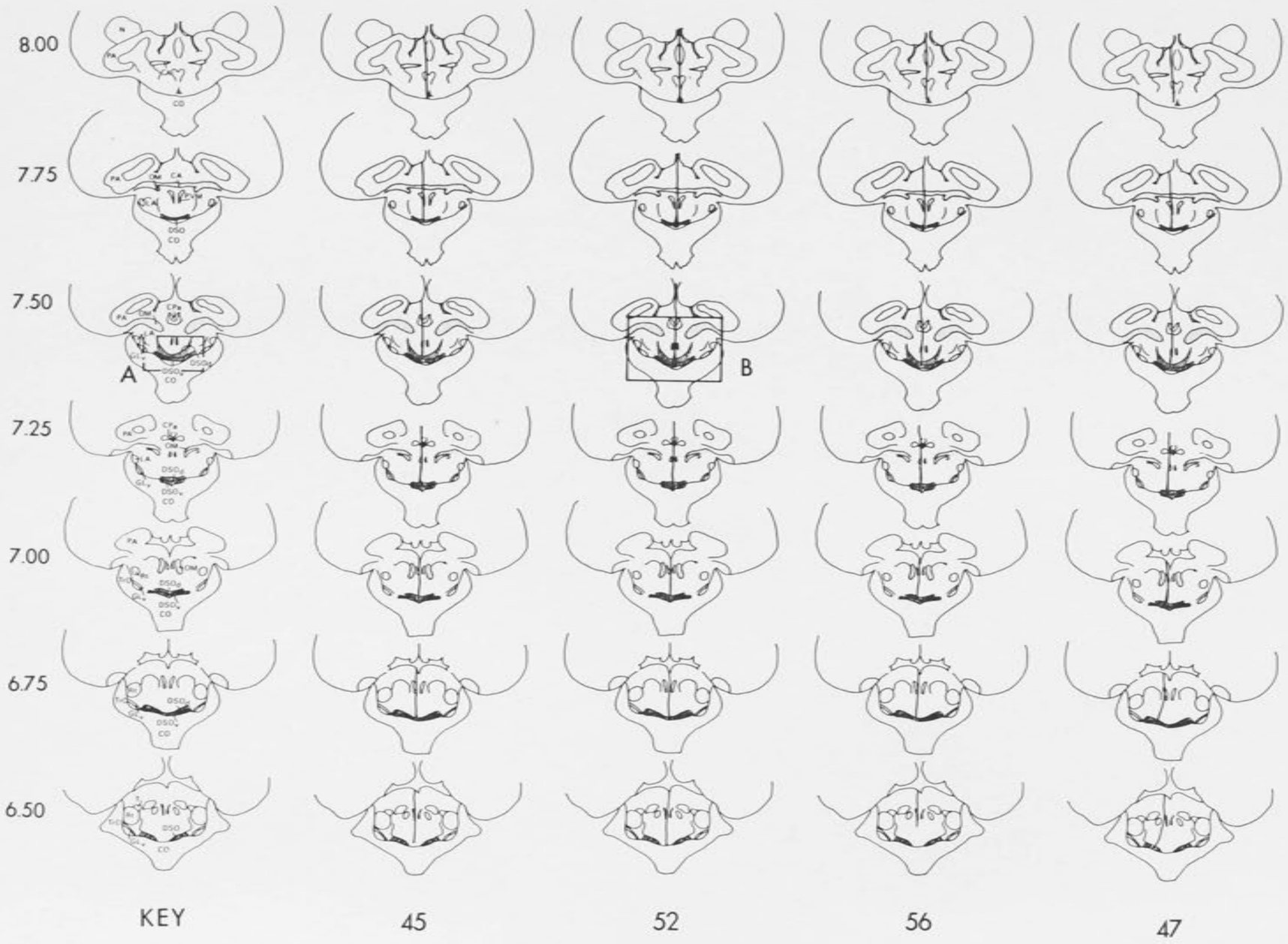
4.3 RESULTS

4.3.1 Anatomical

Reconstructions of the damage to the supraoptic decussation (DSO) and the anterior commissure (CA) after the L1 lesion are shown for all subjects in Figure 4.4. Due to problems with the anaesthetic (see Section 4.2.4.3) a number of birds did not survive the second surgical session (numbers 45, 48, 52 and 64). For each remaining subject, the transection of the posterior and tectal commissures after L3 is shown in Figure 4.5. In both Figures 4.4 and 4.5, the extent of the knife cuts are illustrated with a series of transverse sections. Some selected lesions and an example of the two fibre tract systems in the normal state are shown photographically in Plates 4.1A-F (DSO) and 4.2A-F (CP+CT).

Figure 4.4 The following three pages show the reconstructions of the supraoptic decussation (DSO) and the anterior commissure (CA) after the L1 transection for all subjects. The knife cut is illustrated by the black line passing down the centre of each section. Subject identification numbers are indicated below each series of transverse sections. The first series on each page shows the indentification key to the anatomical structures. The numbers at the left of the key indicate the atlas plate (Karten & Hodos, 1967) to which each section corresponds. Boxed inserts (A-F) are shown photographically in Plates 4.1 A-F.

CA	commissura anterior
CO	chiasma opticum
CPa	commissura pallii
DSO_d	decussatio supraoptica dorsalis
DSO_v	decussatio supraoptica ventralis
GL_v	nucleus geniculatus lateralis pars ventralis
LA	nucleus lateralis anterior thalami
OM	nucleus nervi oculomotorii
PA	paleostriatum augmentatum
PVM	nucleus periventricularis magnocellularis
Rt	nucleus rotundus
T	nucleus triangularis
TrO	tractus opticus
N	neostriatum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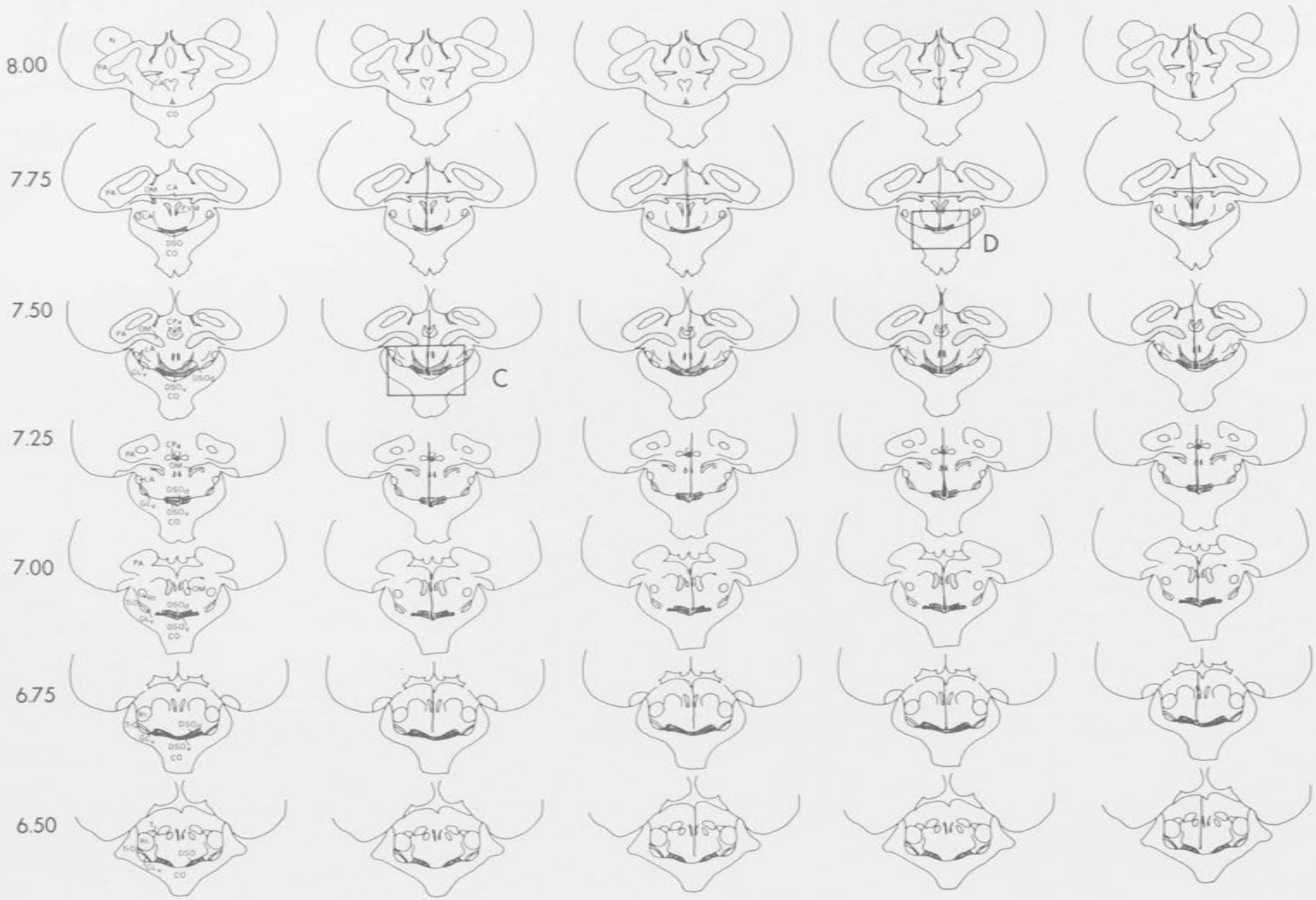
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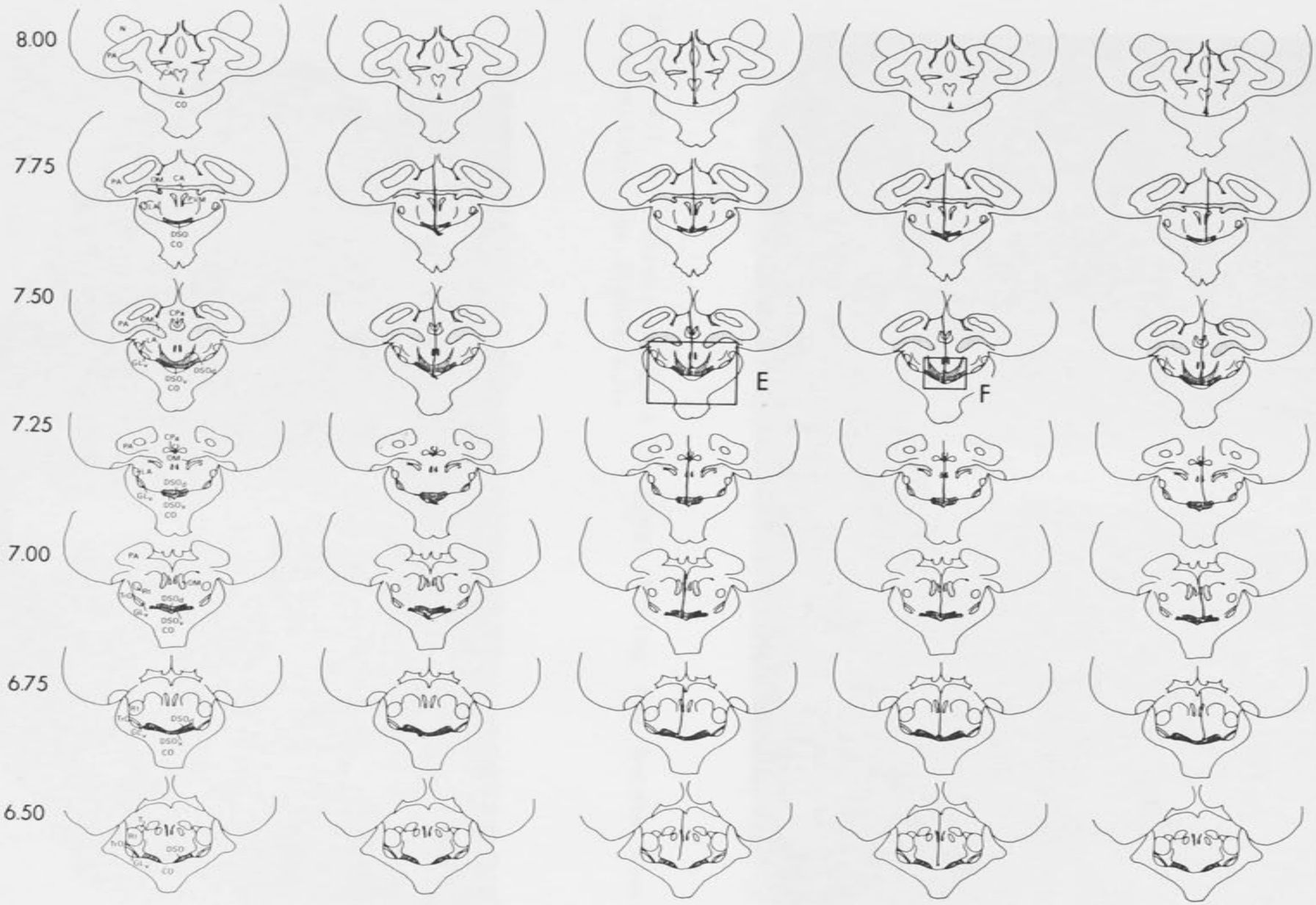
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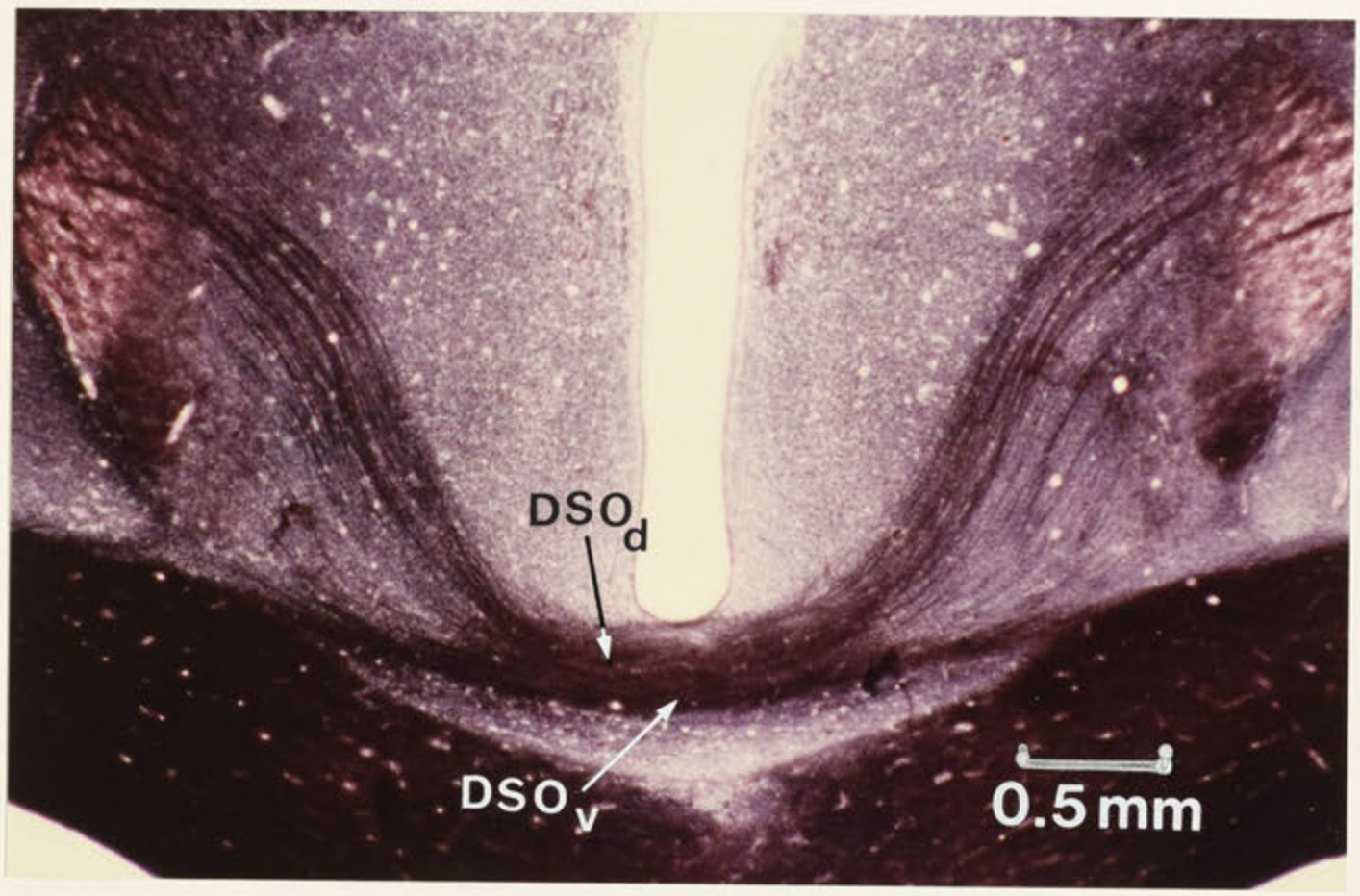


Plate 4.1 A Silver stained section showing the intact supraoptic decussation. See Figure 4.4.

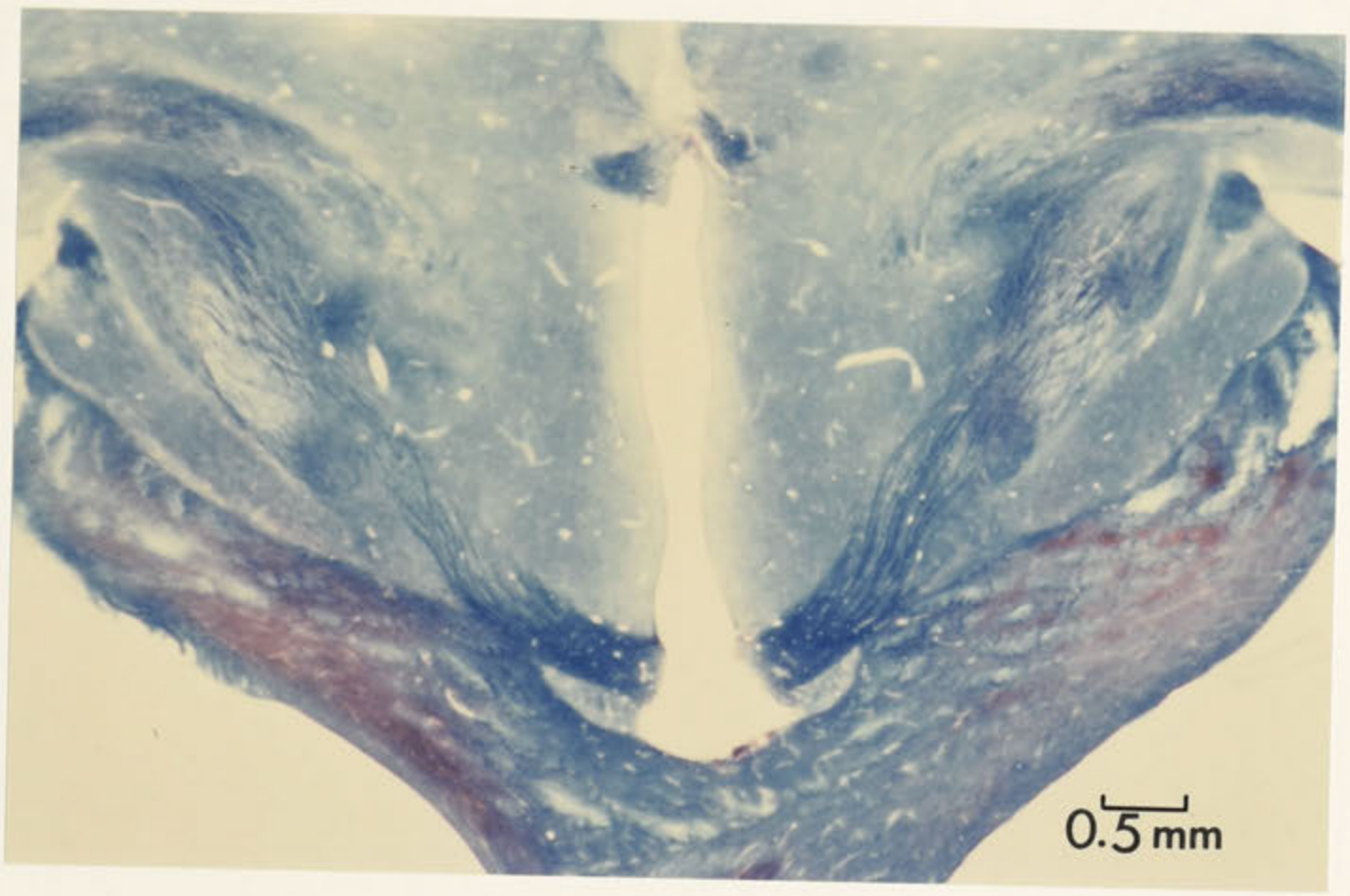


Plate 4.1 B Transection of the supraoptic decussation in subject 52. See Figure 4.4 for details. Section is stained with Luxol Fast Blue (see section 4.2.7).

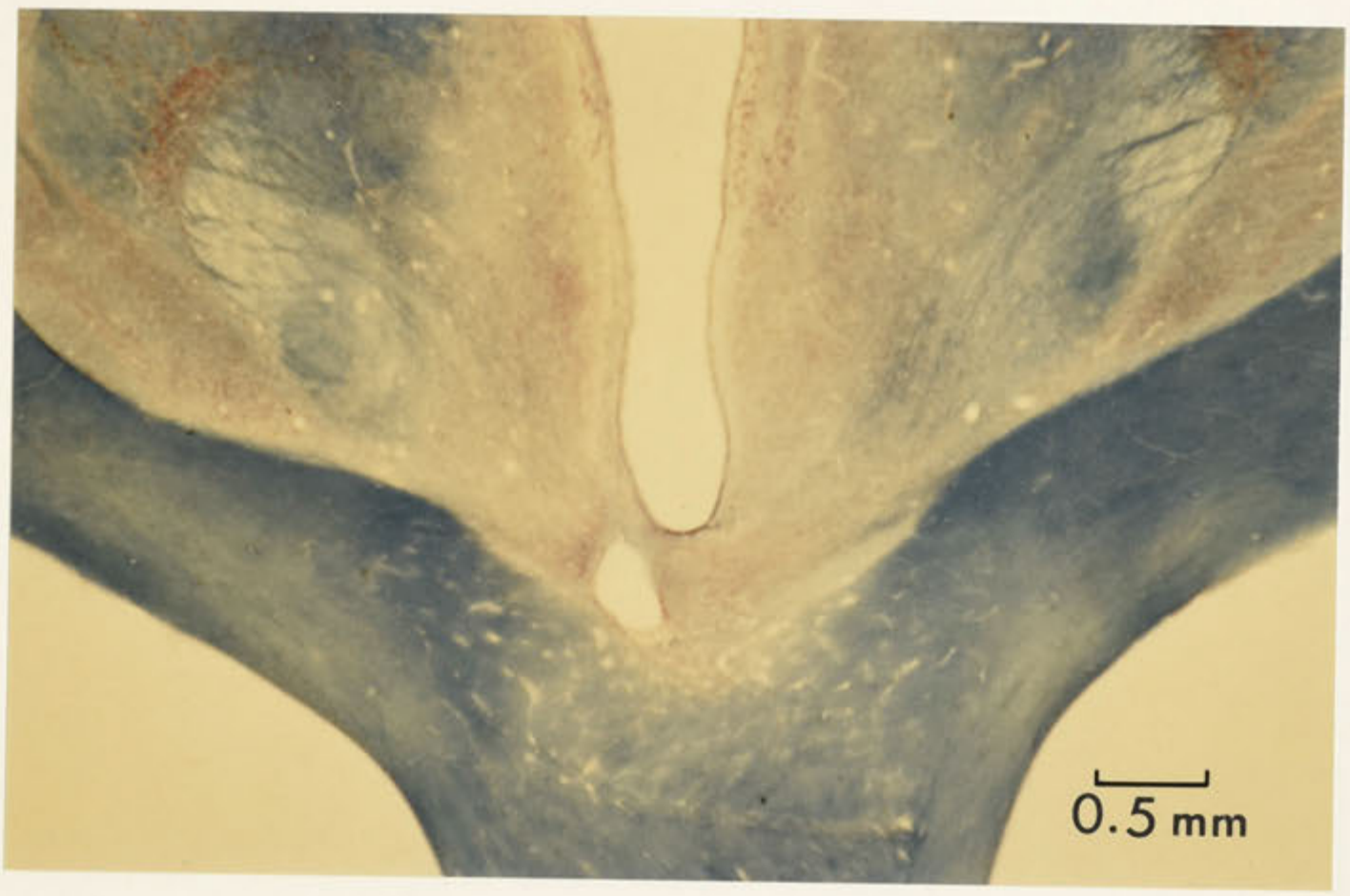


Plate 4.1 C Transection of the supraoptic decussation in subject 37 (see Figure 4.4).

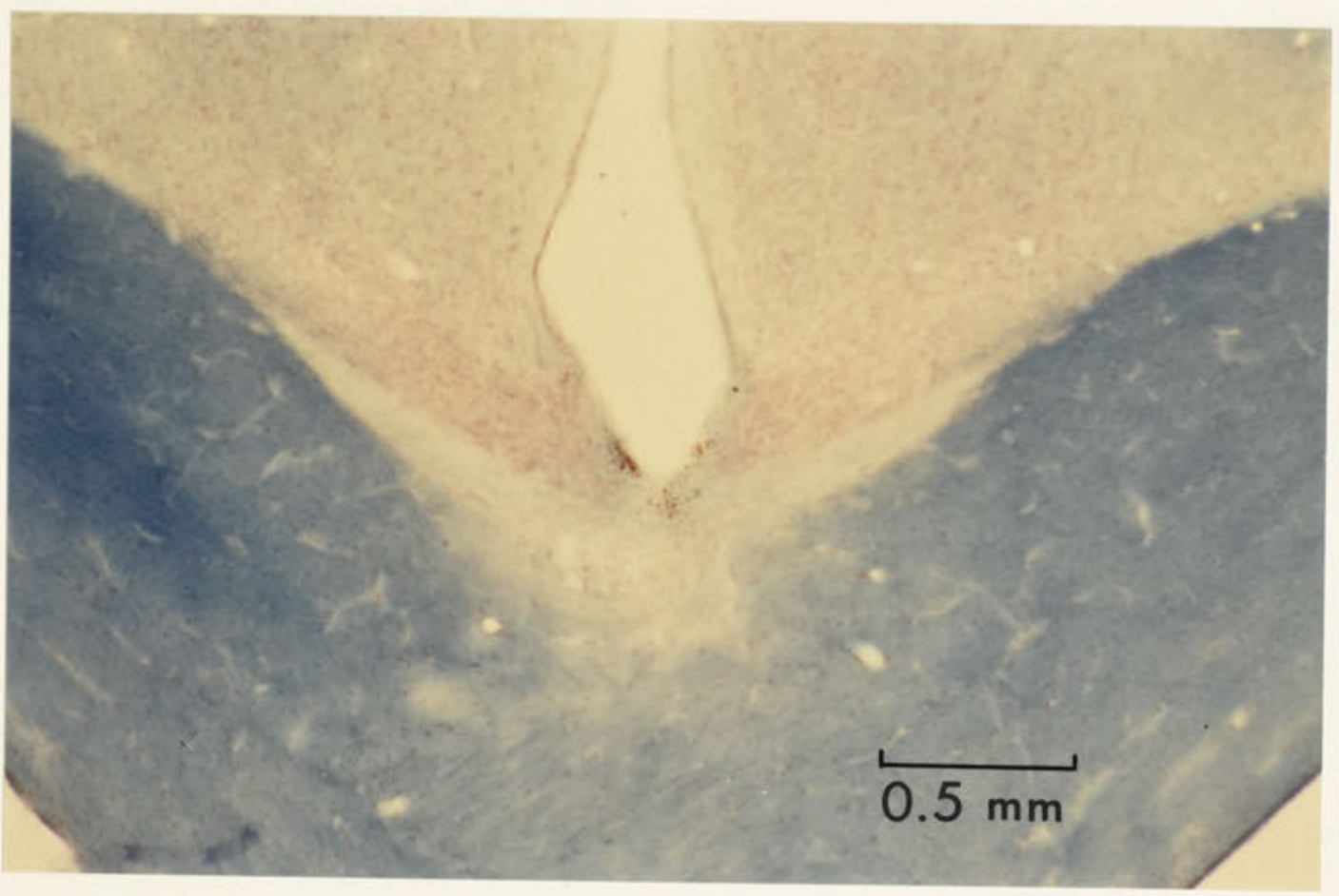


Plate 4.1 D Transection of the supraoptic decussation in subject 57 (see Figure 4.4).

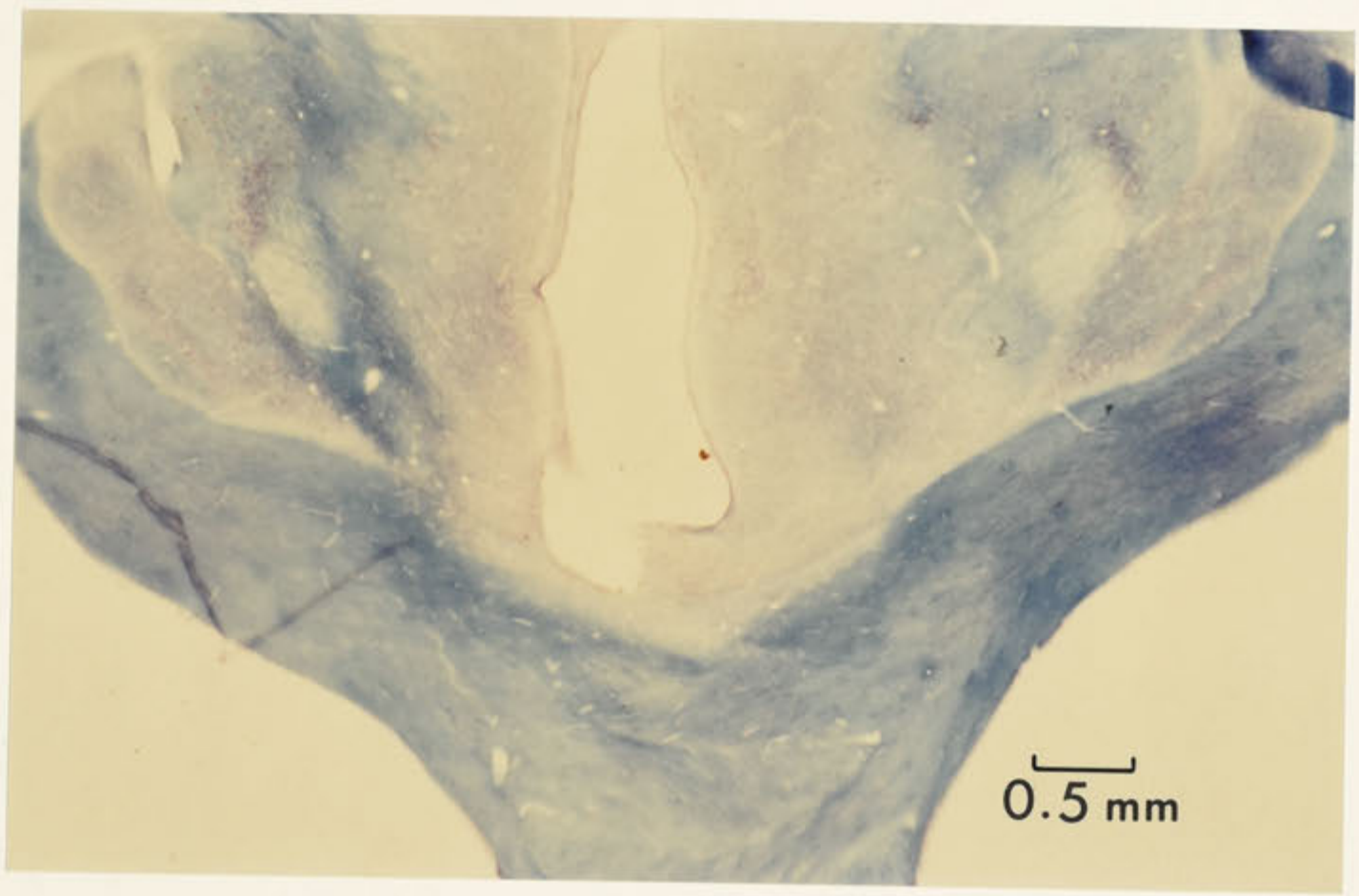


Plate 4.1 E Transection of the supraoptic decussation in subject 64 (see Figure 4.4).

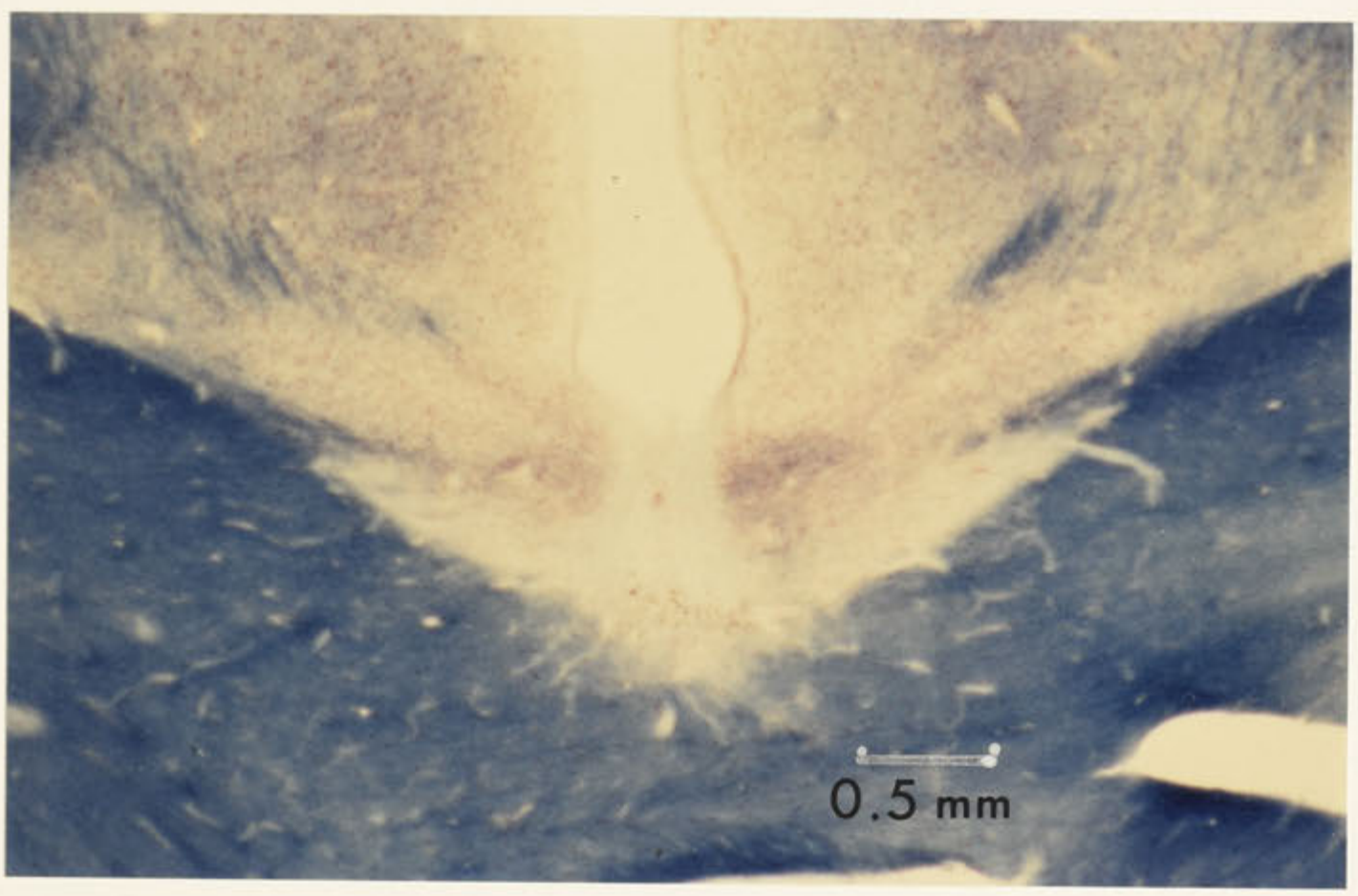
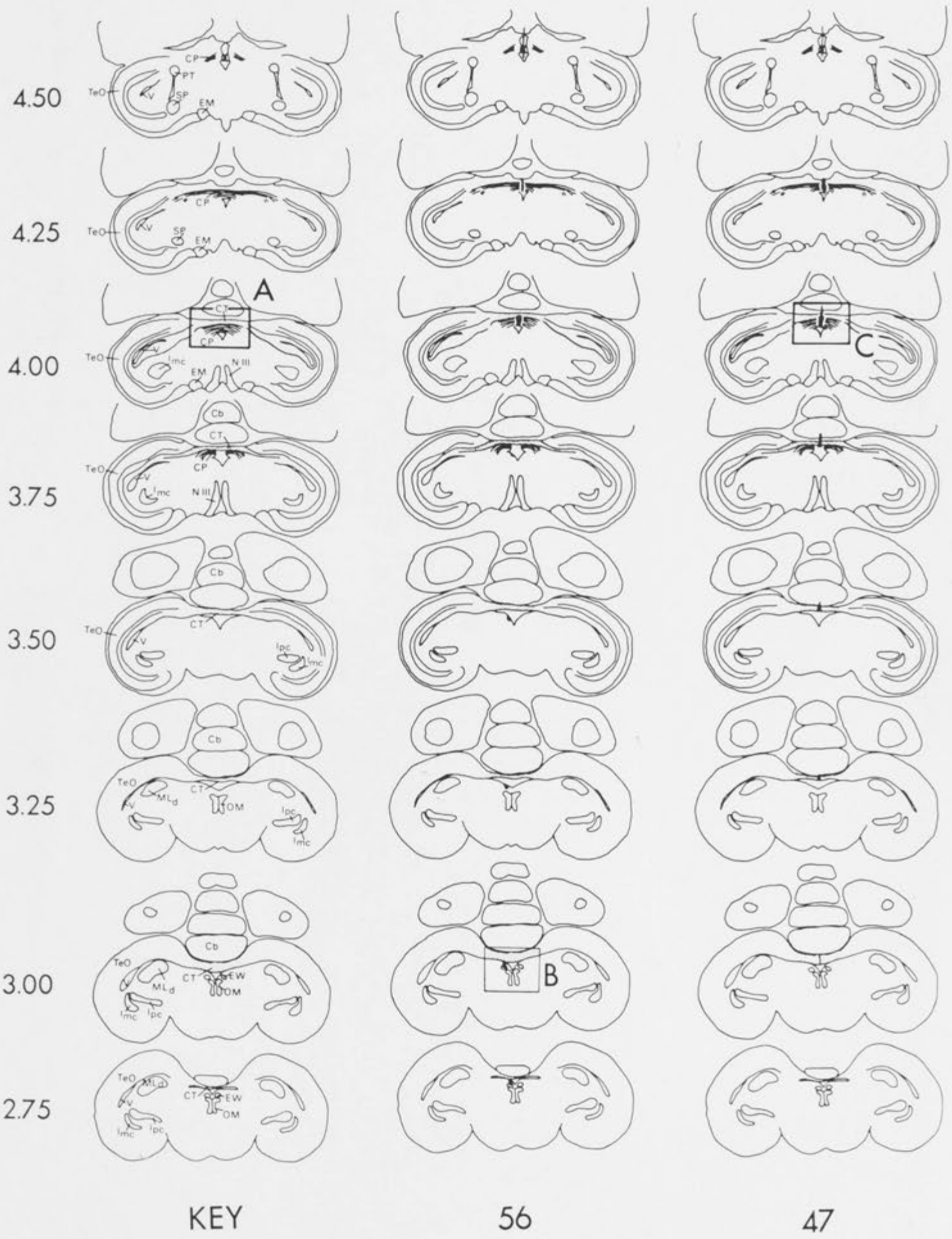


Plate 4.1 F Transection of the supraoptic decussation in subject 48 (see Figure 4.4).

Figure 4.5 The following three pages show the reconstructions of the transection of the posterior and tectal commissures (CP+CT) after the L3 lesion for all subjects. The interruption to the fibres is shown by the black region. Subject identification numbers are shown below each series of transverse sections. An identification key to the anatomical structures is included on each page. The numbers to the left of the key indicate the atlas plate (Karten & Hodos, 1967) to which each section corresponds. Boxed inserts (A-F) are shown photographically in Plates 4.2 A-F.

Cb	cerebellum
CP	commissura posterior
CT	commissura tectalis
EM	nucleus ectomamillaris
EW	nucleus Edinger-Westphal
Imc	nucleus isthmi, pars magnocellularis
Ipc	nucleus isthmi, pars parvocellularis
MLd	nucleus mesencephalicus lateralis, pars dorsalis
N III	nervus oculomotorius
OM	tractus occipitomesencephalicus
PT	nucleus pretectalis
SP	nucleus subpretectalis
TeO	tectum opticum
V	ventriculus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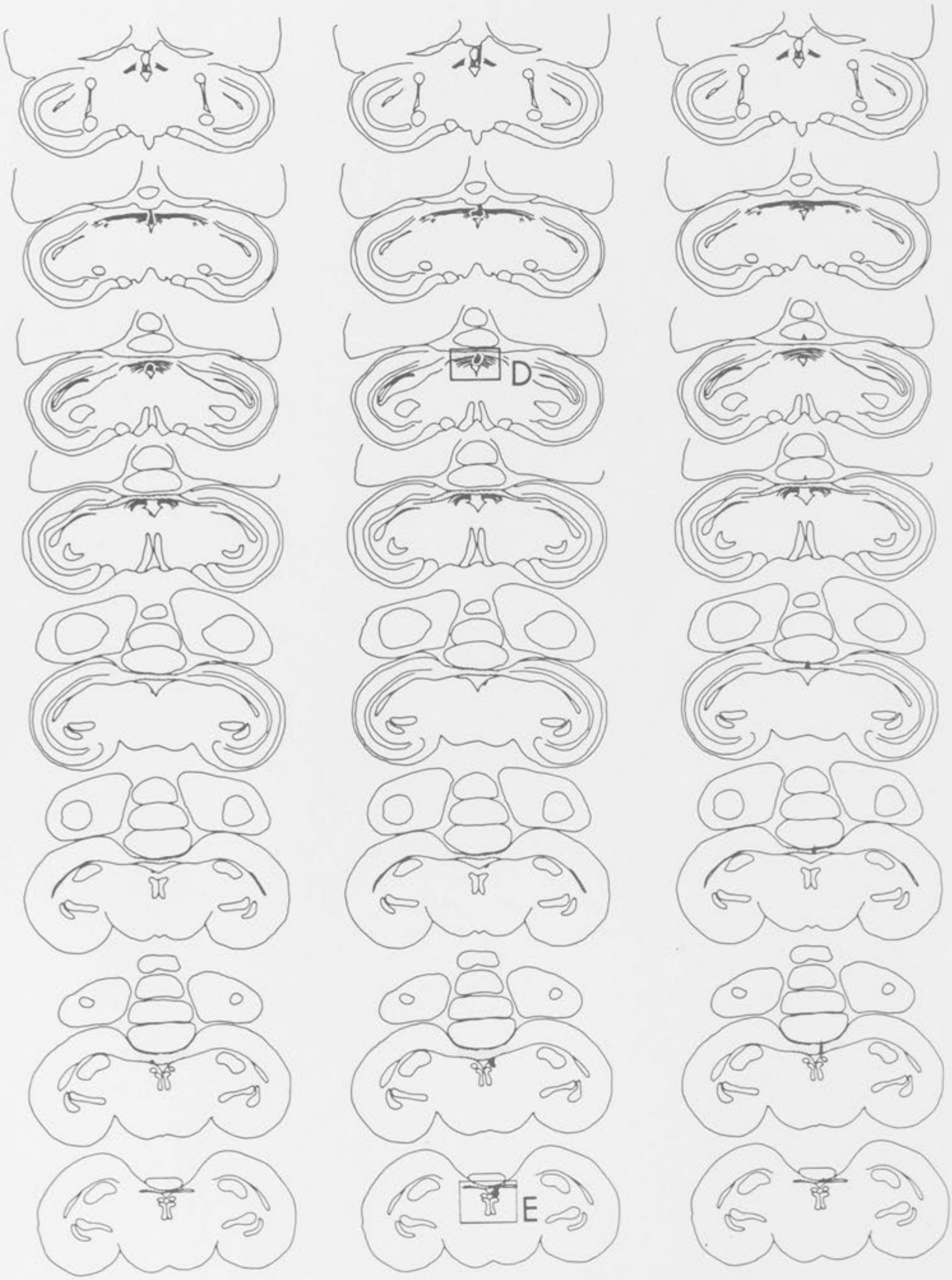

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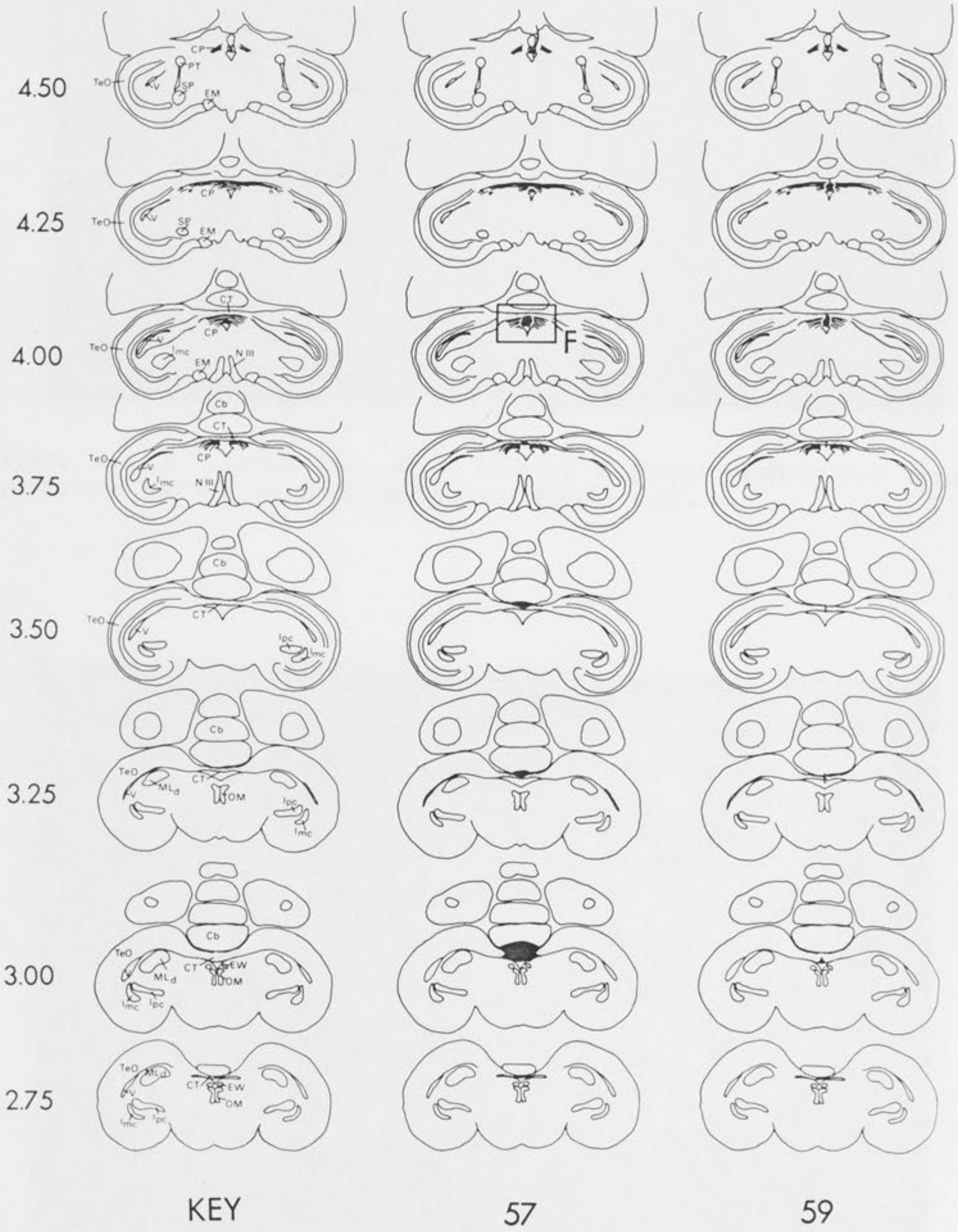
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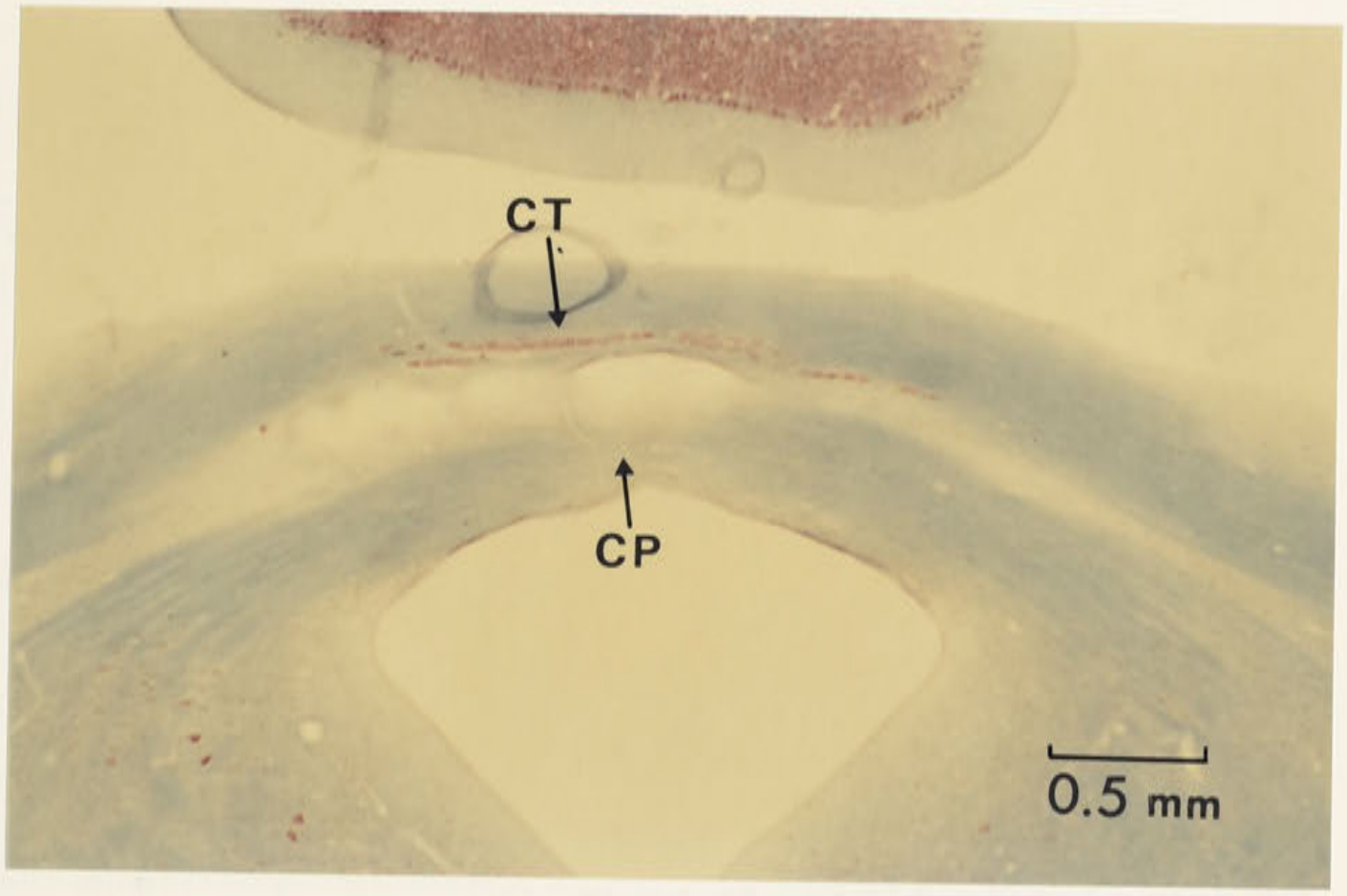


Plate 4.2 A Luxol Fast Blue stained section showing the intact posterior and tectal commissures (see Figure 4.5).

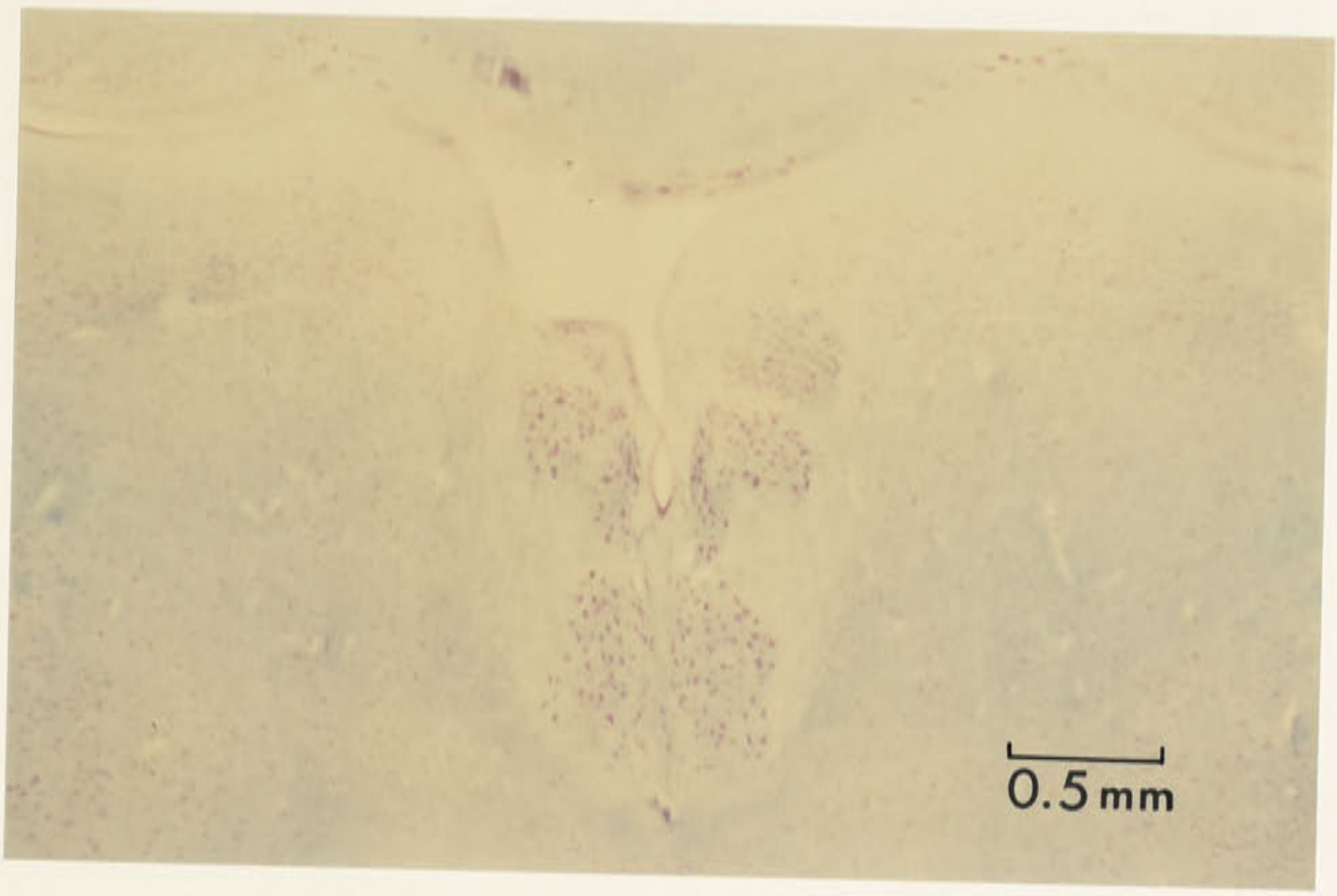


Plate 4.2 B The lesion of the Edinger-Westphal nucleus in subject 56 (see Figure 4.5).

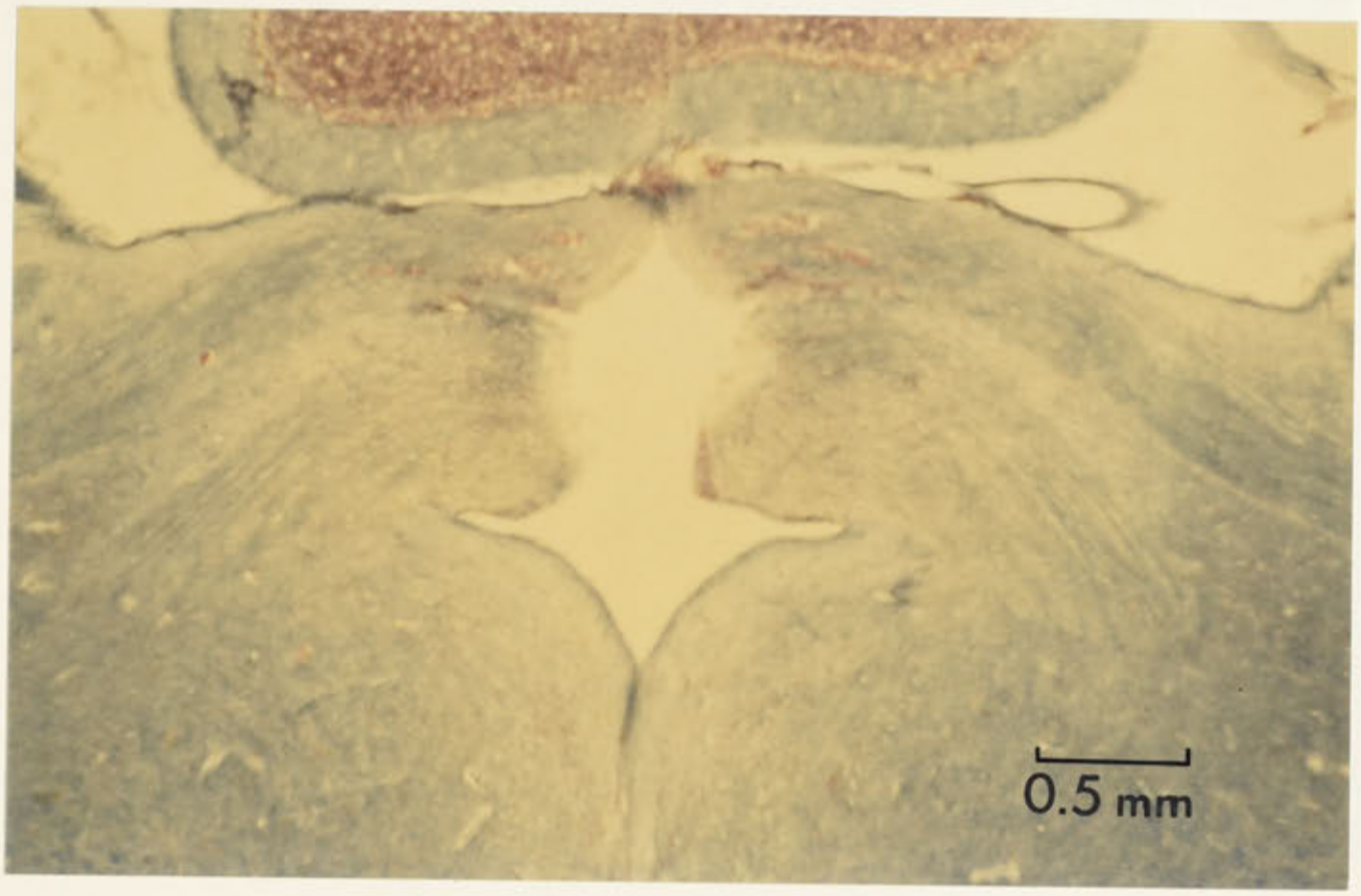


Plate 4.2 C Transection of the posterior and tectal commissures in subject 47 (see Figure 4.5).

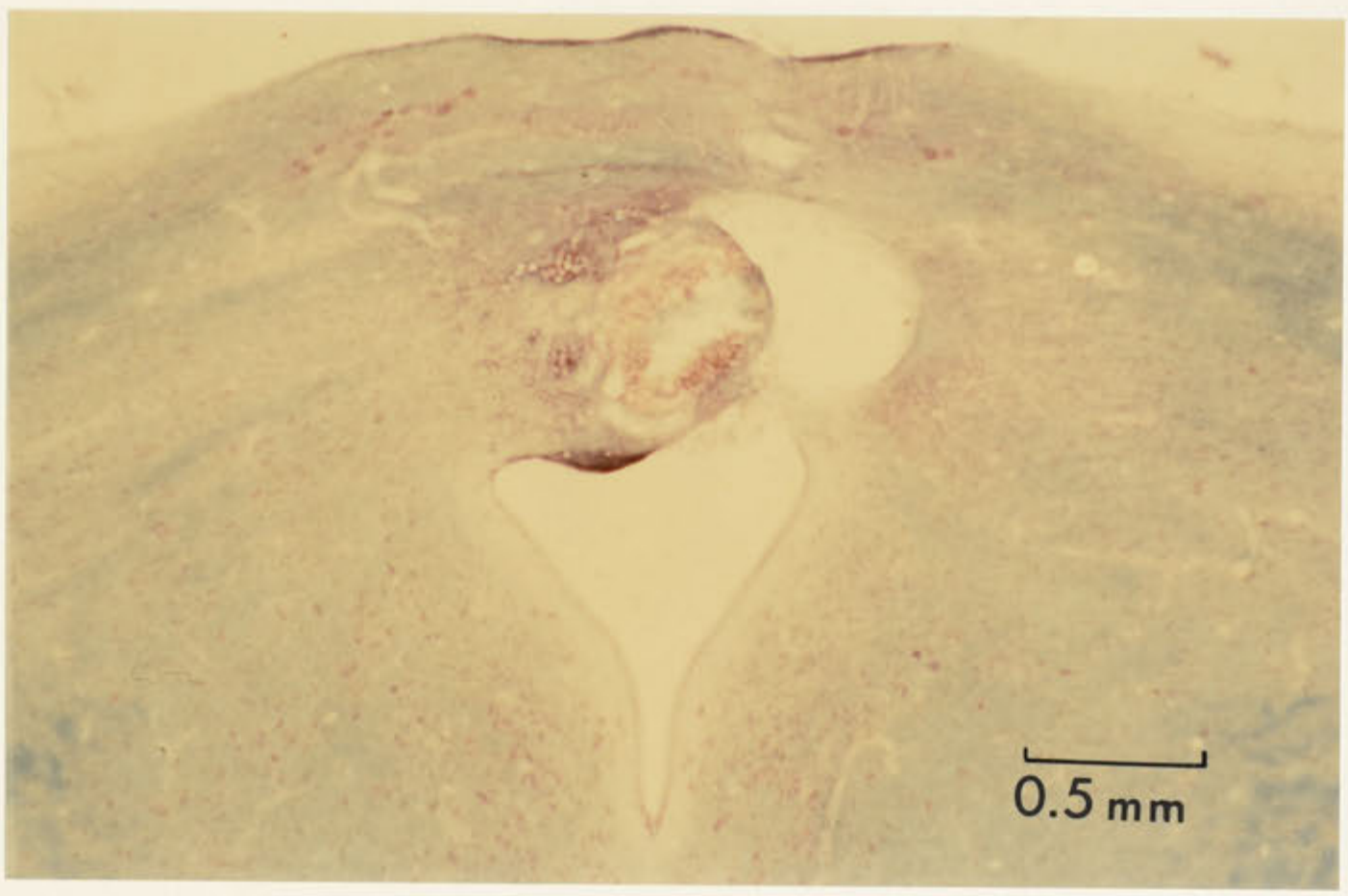


Plate 4.2 D Transection of the posterior commissure in subject 37 (see Figure 4.5).

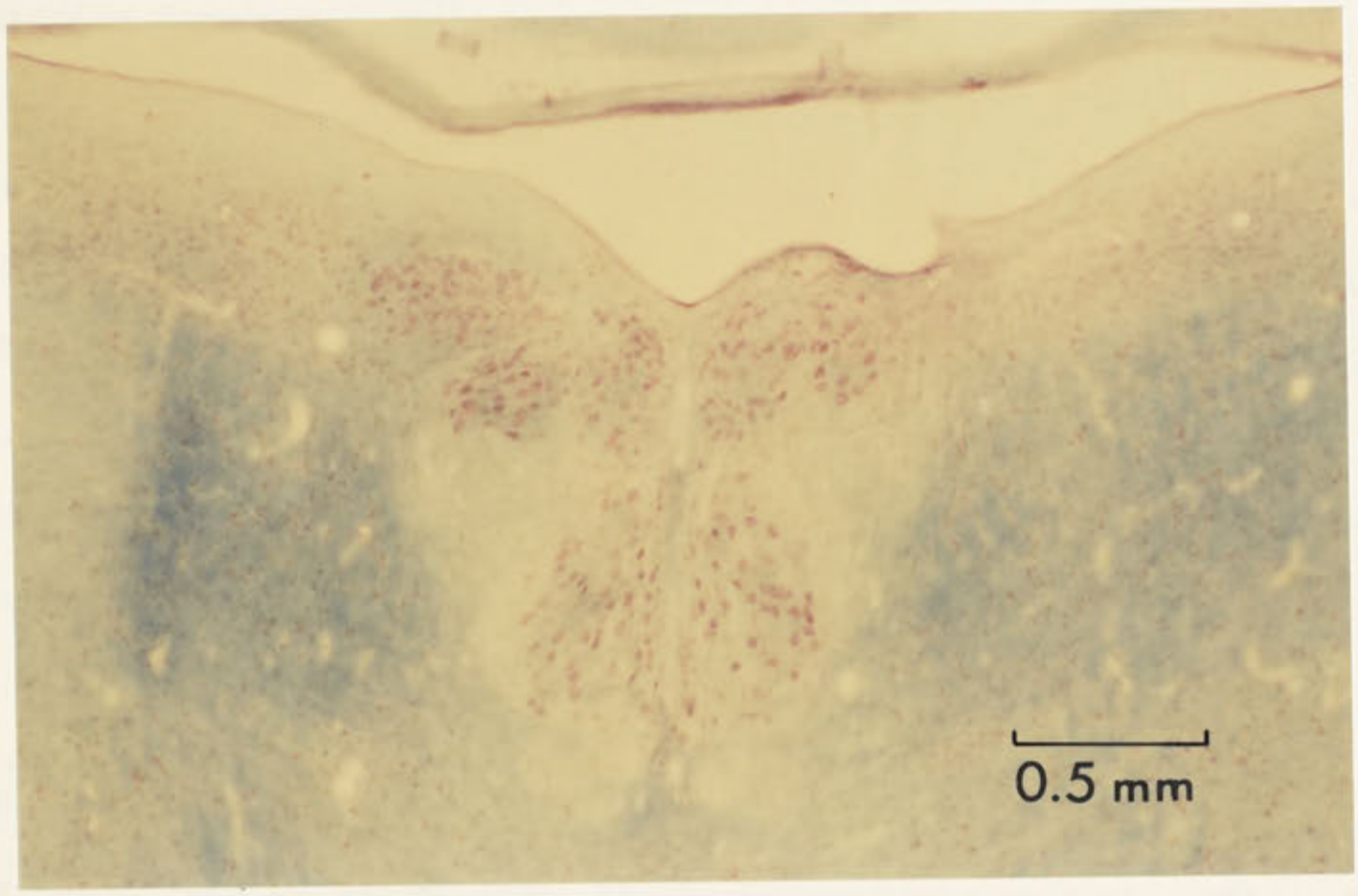


Plate 4.2 E Lesion of the Edinger-Westphal nucleus in subject 37 (see Figure 4.5).

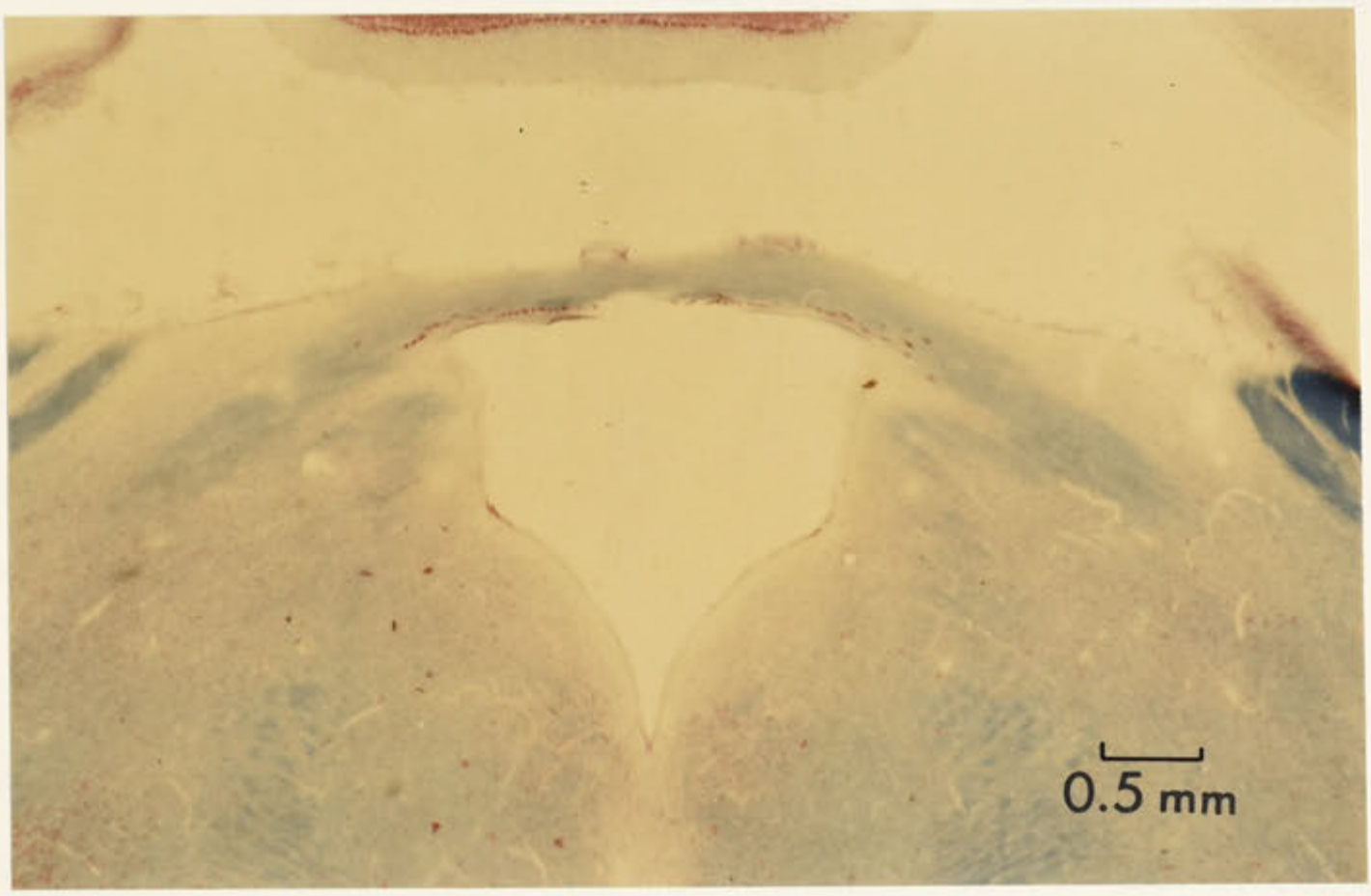


Plate 4.2 F Lesion of the posterior commissure in subject 57 (see Figure 4.5).

4.3.1.1 *Transection of the Supraoptic Decussation (DSO) and/or the Anterior Commissure (CA).*

The extent of the transection of both the ventral (DSO_v) and dorsal (DSO_d) aspects of the DSO and the cut through the CA for each subject, was transposed into a diagrammatic histogram (Figure 4.6). All subjects received complete transection of the CA except number 40. Here the CA was cut at the point where it joins the two occipitomesencephalic tracts (A7.75). Apart from the complete transection of the CA, the sham control birds had no other damage.

Of the experimental birds, the transection was confined to the DSO and CA. Only one subject received damage to the dorsal layers of the optic chiasm which lies immediately ventral to the DSO. This subject (62) was also aberrant in that DSO_d was only slightly damaged, while for all other experimental birds, the dorsal part of the DSO was completely transected. The DSO_v was transected completely in subject 52 and left intact in subjects 45 and 55. The remaining experimental birds tended to have the anterior parts of DSO_v transected.

4.3.1.2 *Transection of the Tectal and Posterior Commissure (CT + CP)*

The extent of the transection of the tectal and posterior commissures for each experimental subject has been transposed into a diagrammatic histogram in Figure 4.7. The three sham birds received no damage to the commissural system.

Transection of the posterior commissure (CP) was generally more complete than of the tectal commissure (CT). Two birds received a complete cut through the anterior-posterior extent of the CT (62 and 47). The CP was completely transected in subjects 37, 47, 56, 58, and 59. Thus, subject 47 had a perfect transection of both the posterior and tectal commissures.

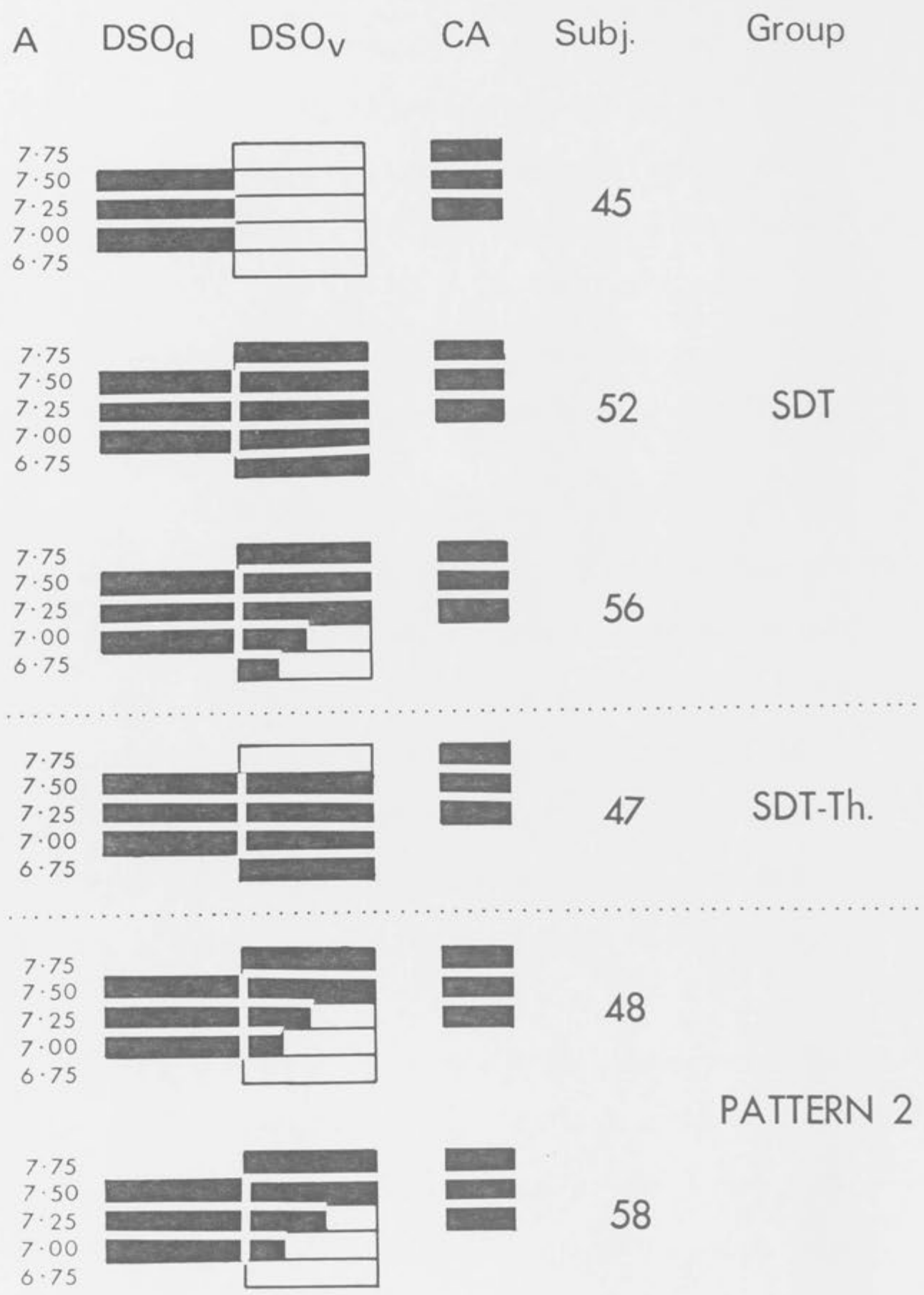


Figure 4.6 A Diagrammatic histogram showing the extent of the transection of the dorsal and ventral aspects of the supraoptic decussation (DSO_d and DSO_v), and the anterior commissure (CA) for all experimental subjects in the SDT, SDT Threshold, and Pattern 2 groups. The AP extent of each fibre bundle (DSO_d, DSO_v and CA) is shown by a series of bars. A blackened bar indicates that the particular fibre bundle was transected at the corresponding A position. Thus it can be seen that the CA extends from A 7.75 to A 7.25 and was completely transected in all subjects. Subject 62 also had damage to the dorsal layers of the optic chiasm (CO).

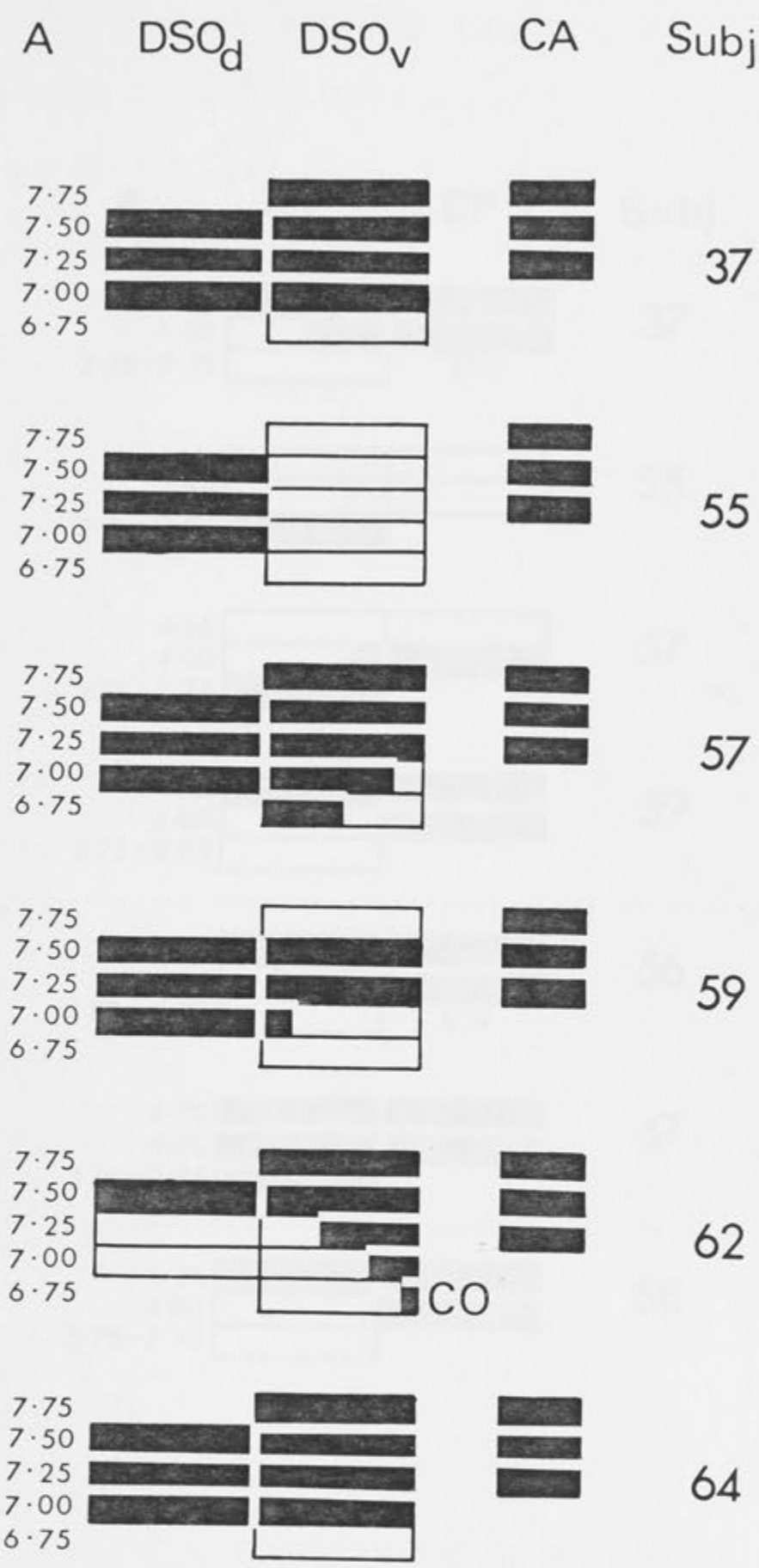


Figure 4.6 B Diagrammatic histogram showing the extent of the transection of the DSO and CA for all subjects in the LACE group.

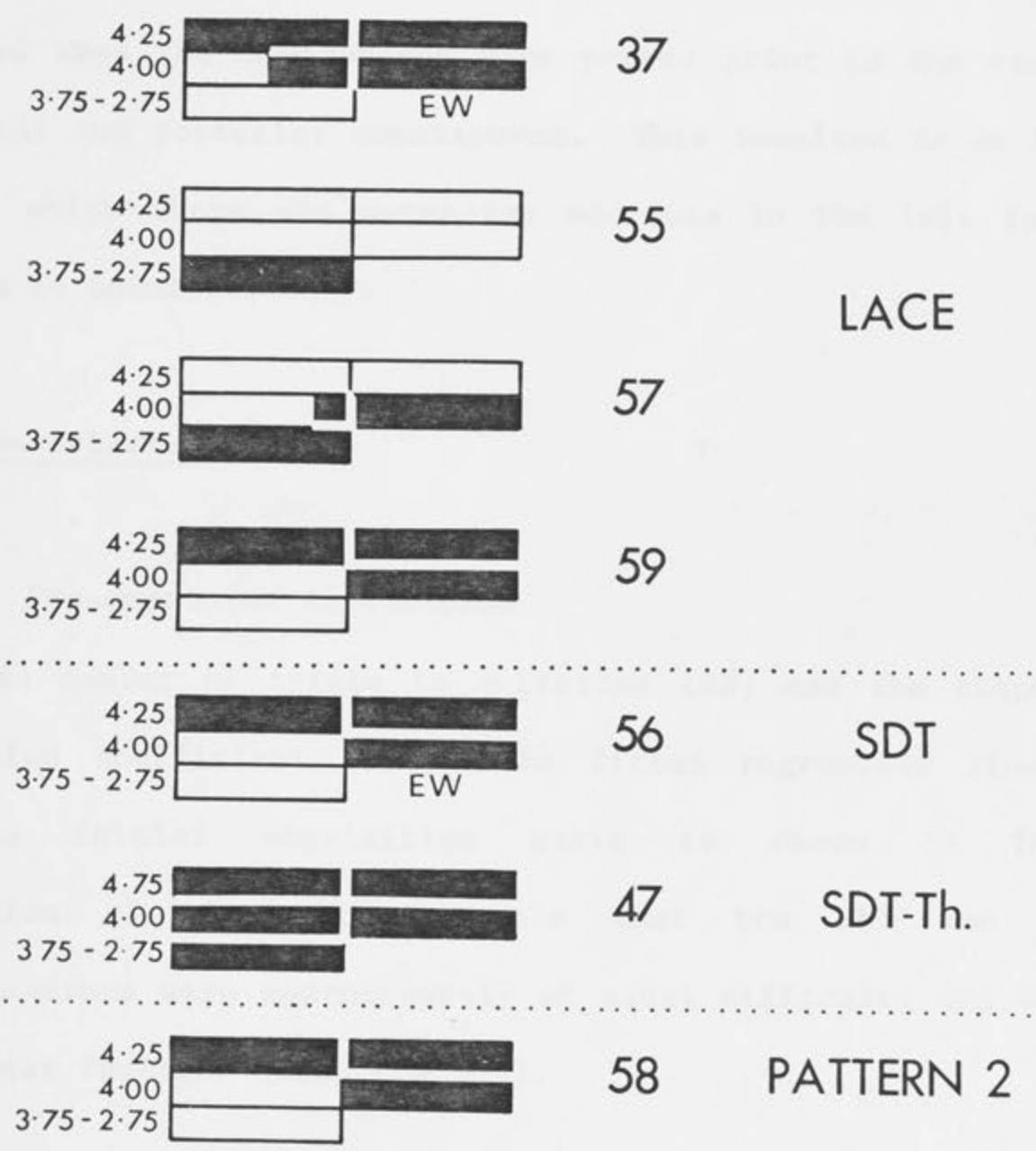


Figure 4.7 Diagrammatic histogram showing the extent of the transection of the posterior (CP) and tectal commissures (CT) for all subjects that received the second surgical session (L3). See caption to figure 4.6 for interpretation. Subjects 37 and 56 also had unilateral lesions of the Edinger-Westphal (EW) nucleus.

Knife cuts were confined to the CP and CT for all experimental birds except two subjects which also received discrete unilateral lesions of the Edinger-Westphal nucleus (EW). The right EW was completely lesioned in subject 37 (plate 4.2C) and partially in subject 56 (plate 4.2F). In one bird (number 55) the left ventricle collapsed when the hemispheres were parted prior to the sectioning of the tectal and posterior commissures. This resulted in an interesting case in which there was extensive necrosis in the left forebrain in addition to commissurotomy.

4.3.2 Behavioural

4.3.2.1 *Pre-Operative Acquisition*

The number of trials to criterion (SN) and the slope (SL) and correlation coefficient (r) of the fitted regression line for each subject's initial acquisition curve is shown in Table 4.2. Examination of this data reveals that the SDT and Pattern 2 discriminations were approximately of equal difficulty and well fitted by a linear function (mean r = .94).

The LACE discrimination learning curves were not as linear (mean r = .88) as the SDT and Pattern 2 discriminations, particularly considering r was based upon a larger SN. The greater number of sessions taken to reach criterion by birds in the LACE task group was readily apparent when compared with the SDT and Pattern 2 groups combined (mean SN_{LACE} = 22.6; mean $SN_{PATTERN/SDT}$ = 14.8) and was accompanied by lower values for SL (mean SL_{LACE} = 2.1; MEAN $SL_{PATTERN/SDT}$ = 4.7). The LACE task acquisition curves were significantly slower than the other groups (SL: $t = 3.18$, $p < .005$; SN: $t = 2.65$, $p < .025$; $df = 11$). This difference was increased when the acquisition curves of the LACE task group were compared against

the acquisition curves for the SDT reported in chapter 2 (see Section 2.3.1.2). The difference was too extreme to be attributed to seasonal variation. Rather, it would appear that the LACE task was more difficult for the birds to learn than the SDT.

Group	Subject Number	SN	SL	r
SDT	45	13	4.8	.97
	52	9	7.9	.94
	56	28	1.5	.93
PATTERN 2	48	10	4.7	.92
	58	12	4.4	.95
LACE	37	24	1.5	.95
	55	22	1.7	.87
	57	19	2.8	.86
	62	24	2.1	.90
	64	21	2.6	.93
	59	30	1.9	.90
	67	20	2.5	.86
	68	21	1.5	.81

Table 4.2 Parameters of the initial acquisition curves for the three discriminations SDT, Pattern 2 and LACE task. SN, number of trials to criterion; SL, slope of the fitted regression line; r, correlation coefficient of the fitted regression line.

4.3.2.2 *Cue Controls*

All six subjects tested, except the SDT bird (number 56), attained mean scores greater than 90% correct during the flip control session. The performance of subject 56 fell to 54% and 57% during two successive sessions of the flip control. This subject was then given one normal session (during which mean performance was 96%) prior to the second control session (i.e. monocular cue simulation). No subject attained scores significantly greater than chance during the second control session. The mean score for all subjects was 58% (Standard error = 1.4). Hence all subjects were unable to generalise from the real depth task to a simulation of depth produced by monocular cues such as overlay and static motion parallax.

4.3.2.3 *Post-Operative Testing*

Subjects did not show any change in general behaviour, locomotion or posture after either surgical session, and appeared eager to work in the operant chamber.

Recall that during the first surgical session, cuts were made through the supraoptic decussation (DSO) and the anterior commissure (CA) in experimental birds (L1) while sham subjects received lesions to the CA alone (L2). During the second surgical session, additional cuts were made through the posterior and tectal commissures (CP and CT) in the experimental birds (L3), while control subjects only received a sham lesion (L4).

The initial acquisition (pre-operative), post-operative I and post-operative II performance curves for each subject (except the threshold birds) are shown in Figures 4.8, 4.9 and 4.10. The performance curves for the SDT experimental birds are shown in Figure 4.8, the Pattern 2 experimental and LACE task sham subjects in Figure

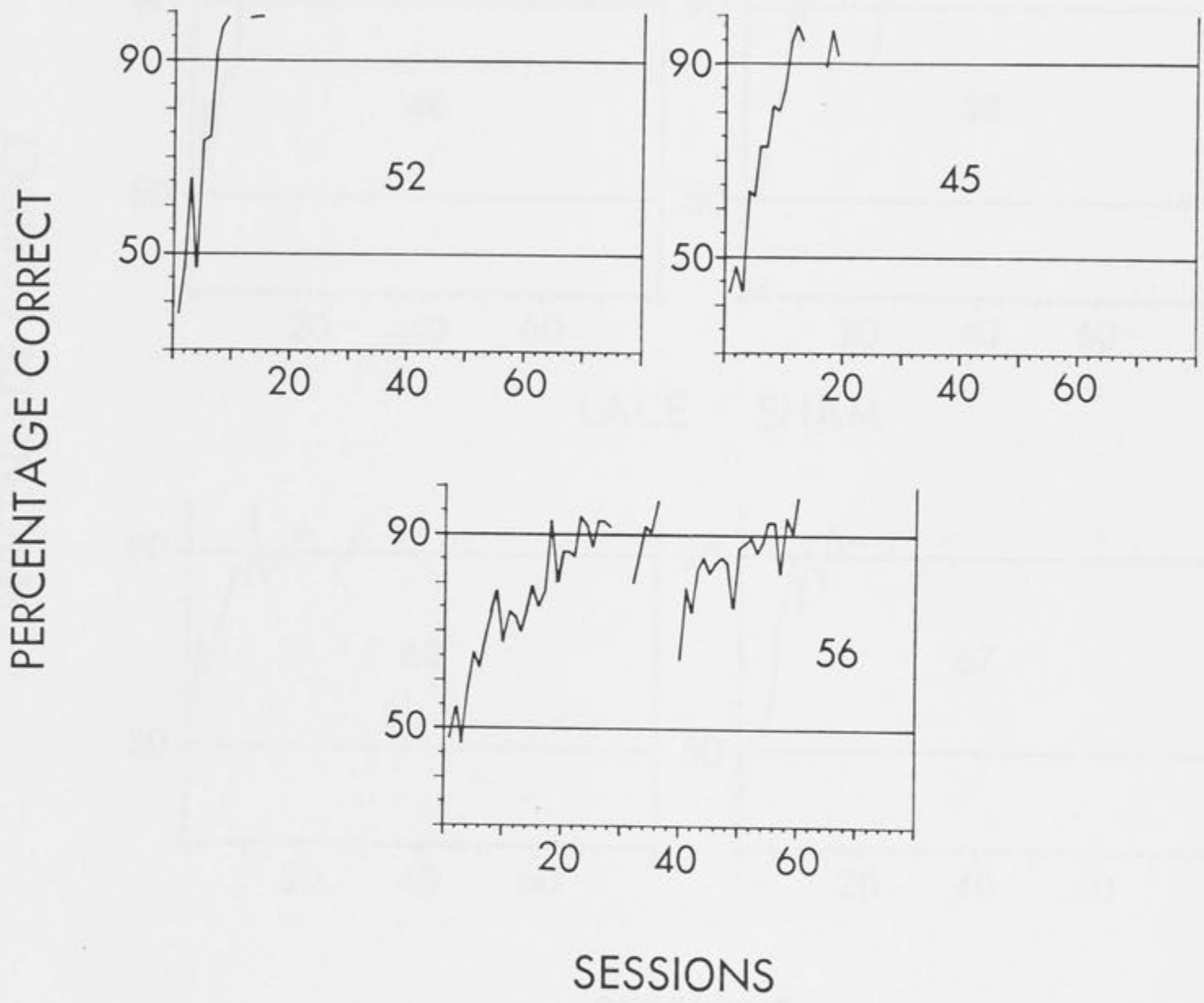


Figure 4.8 The initial aquisition and post-operative performance for the SDT experimental birds. All subjects were tested after transection of the DSO and CA (post-operative I). Subject 56 was also subsequently tested after the CP and CT were transected (post-operative II). The horizontal lines drawn across each graph indicate the 50% (chance performance) and 90% (criterion performance) correct levels.

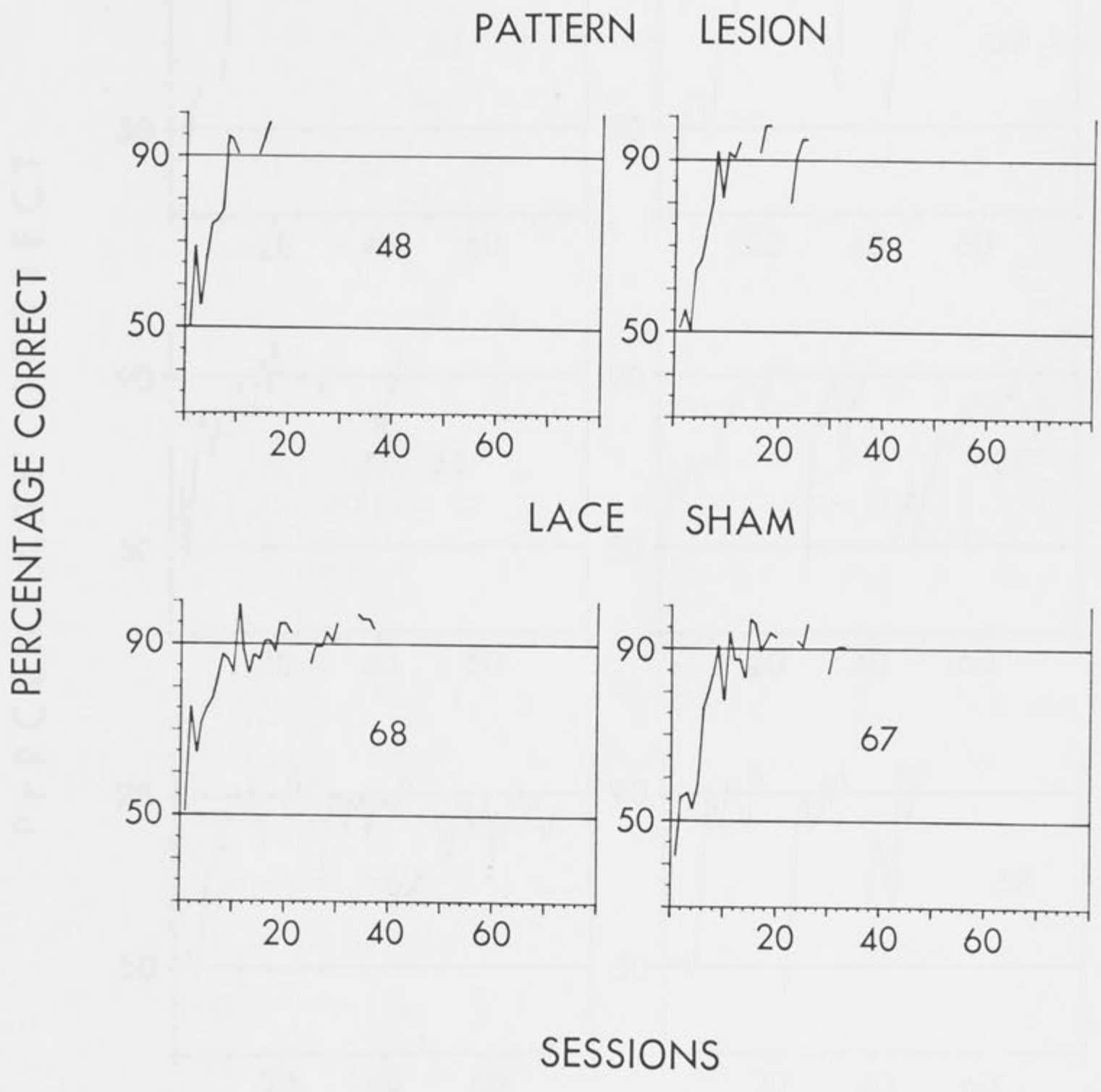


Figure 4.9 The initial acquisition and post-operative performance for the birds trained on the pattern 2 discrimination (48 and 58) and given L1 (DSO and CA) followed by L3 (CT and CP, 58 only) transections; or trained on the LACE task and given sham lesions. The breaks in each subject's graph indicates the time at which surgery was done.

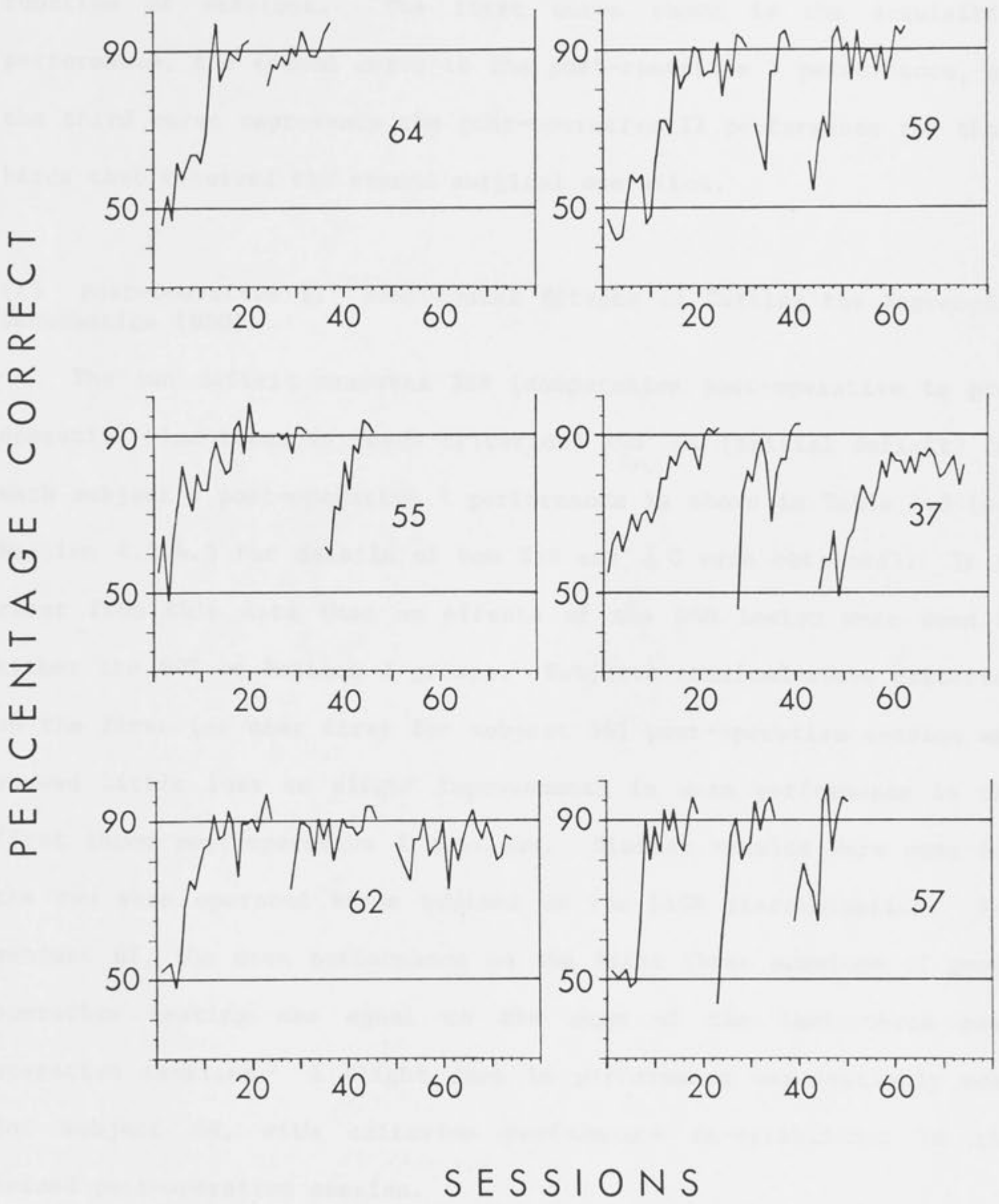


Figure 4.10 The initial acquisition (first curve), post-operative I (second curve) and post-operative II (third curve except subject 64) performance for all birds trained on the LACE task.

4.9, and the LACE task sham subjects in Figure 4.10. The graph for each individual bird shows the percentage correct score obtained as a function of sessions. The first curve shown is the acquisition performance, the second curve is the post-operative I performance, and the third curve represents the post-operative II performance for those birds that received the second surgical operation.

(i) Post-Operative I. Behavioural Effects of Cutting the Supraoptic Decussation (DSO):

The two deficit measures %SN (comparative post-operative to pre-operative time taken to reach criterion) and ΔC (initial deficit) for each subject's post-operative I performance is shown in Table 4.3 (see Section 4.2.4.3 for details of how %SN and ΔC were obtained). It is clear from this data that no effects of the DSO lesion were seen in either the SDT or Pattern 2 groups. Subjects remained above criterion on the first (or near first for subject 56) post-operative session and showed little loss or slight improvements in mean performance in the first three post-operative I sessions. Similar results were seen for the two sham operated birds trained on the LACE discrimination. For subject 67, the mean performance on the first three sessions of post-operative testing was equal to the mean of the last three pre-operative sessions. A slight drop in performance was initially seen for subject 68, with criterion performance re-established in the second post-operative session.

Group	Subject Number	%SN	Δ C	D
SDT	45	0	-3	0
	52	0	+3	0
	56	8	-7	1
PATTERN 2	48	0	+1	0
	58	0	+4	0
LACE	37	52	-24	13
	55	21	-3	1
	57	63	-34	21
	62	76	-12	9
	64	67	-8	5
	59	15	-21	3
LACE/SHAM	67	0	0	0
	68	17	-6	1

Table 4.3 Estimate of deficits in performance after lesions to DSO+CA (subjects 45-59) or to CA alone (subjects 67, 68): %SN, percentage of pre-operative trials taken to reach criterion post-operatively; Δ C, change in initial post-operative performance relative to criterion; D, gross estimate of relative behavioural deficit (see text for full explanation).

In contrast to the results for the SDT, Pattern 2 and LACE/Sham groups, the DSO lesion temporarily affected the performance of the birds trained on the LACE task. This was particularly noticeable for subjects 37, 57, 62 and 64. Initial post-operative performance was retarded for all experimental birds trained on the LACE task, except subjects 55 and 64. An overall estimate of the relative deficit

calculated from the measures %SN and Δ C, was found by:

$$\text{Behavioural Deficit (D)} = \frac{\%SN \times \Delta C}{100}$$

In Table 4.3, it can be seen that the behavioural deficits were greatest for subjects 57 and 37. These subjects also had the most complete transection of DSO_v. Furthermore, subject 55 showed no deficit relative to the sham operated birds and was the only bird trained on the LACE task in which DSO_v was left intact. In contrast, little consistency was shown in the behavioural deficits for subjects 57 and 55, both of whom had complete transection of DSO_d.

The behavioural deficits cannot be attributed to the anterior commissure (CA) lesion, as this commissure was cut in the sham control birds with no resultant behavioural effect. Thus the behavioural deficits on the LACE task were correlated with transection of the dorsal aspect of the DSO.

(ii) Post-Operative II. Behavioural Effects of Cutting the Posterior and Tectal Commissures (CP + CT) in addition to the DSO:

The two deficit measures %SN (comparative post-operative to pre-operative time taken to reach criterion) and Δ C (initial deficit) for each subjects' post-operative II performance is shown in Table 4.4 (see Section 4.2.4.3 for details of how %SN and Δ C were obtained).

Group	Subject Number	%SN	Δ C	D
LACE	37	-	-35	Permanent
	55	42	-29	12
	57	56	-21	12
	59	64	-32	21
	62	-	-21	Permanent
LACE/SHAM	67	7	-2	0
	68	0	+2	0
PATTERN 2	58	0	-4	0
SDT	56	72	-20	14

Table 4.4 Estimates of the deficits in performance after the second surgical session: %SN, percentage of pre-operative sessions taken to reach criterion post-operatively; Δ C, change in initial post-operative performance relative to criterion; D, gross estimate of relative behavioural deficit (see text for details).

It is clear from this data that as with the DSO lesion results, no deficits in performance occurred for the Pattern 2 or LACE sham control groups. In contrast, all subjects trained on a depth task showed behavioural deficits after commissurotomy.

For two of the subjects (37 and 62), the deficits were permanent. Relearning did not reach criterion after 31 and 27 sessions respectively (approximately 3,000 trials). Subject 62 also had a small lesion in the dorsal layers of the optic chiasm.

Nevertheless, the deficit also reflects the effects of the transection of CP + CT, as this bird was able to reach criterion prior to the second surgical session. Afterwards however, performance remained unstable. Subject 37 had an extensive commissurotomy in addition to a complete unilateral lesion of the Edinger Westphal nucleus (EW). The behavioural deficit caused by a similar lesion was also evident in the post-operative II performance of subject 56. This subject did, however, eventually manage to relearn the SDT to criterion.

For the remaining birds that were tested on the LACE discrimination, the largest deficit was seen in subject 59, who also received the most extensive CP lesion. Anterior lesions of the commissural system at the tectal level, particularly involving transection of CP, appear to be in best accord with the behavioural deficits.

4.3.3 Effect of Commissurotomy on Depth Thresholds

Recall that subject 47 received a perfect transection of both CA + DSO, and CP + CT. In contrast, the sham control (subject 40), only received partial transection of the anterior commissure. The normal threshold attained, and the threshold performance after both surgical sessions for each subject are plotted in Figure 4.11. The development of the threshold was plotted in terms of retinal disparity in minutes of arc over time as described in Section 3.3.2.3, Method 1.

The normal threshold achieved by subject 47 prior to surgery was 12 mins of arc. This was unlikely to be the minimum possible which was described in Section 3.3.2.3 as more of the order of 1 min of arc. It would appear that this subject was from the population mentioned in Chapter 2, in which the binocular depth acuity was lower than the maximum possible.

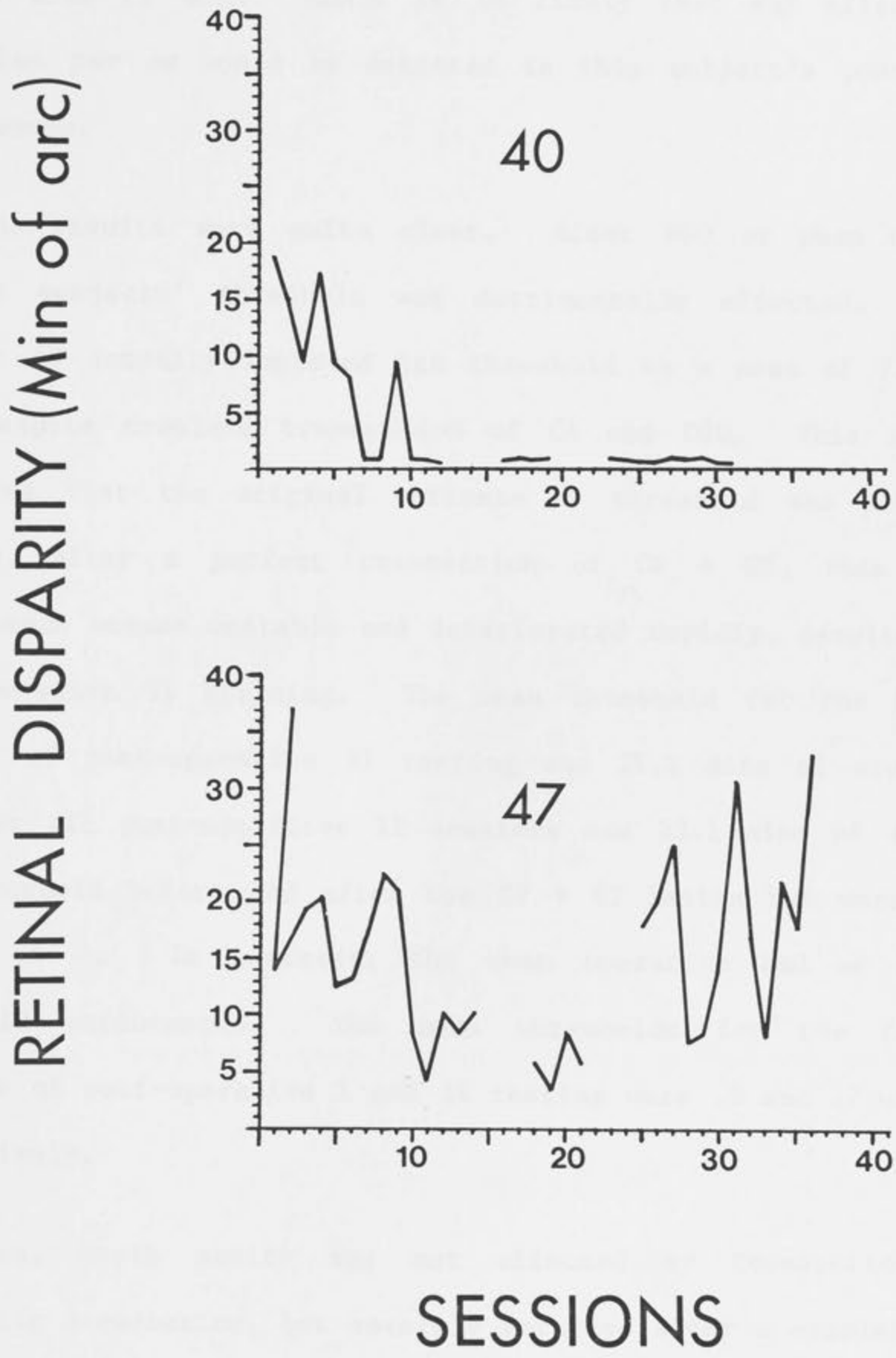


Figure 4.11 The development of the depth threshold measured on the SDT (first curve) in terms of retinal disparity in minutes of arc for subjects 40 and 47. The second segment shows the threshold obtained after either DSO and CA (47) or CA alone (40) were transected. The third segment in each subject's graph shows the performance after CP and CT were transected (47) or a sham operation only (40). The sham birds performance (top graph) was not effected by the surgical manipulations and the threshold remained stable. The lesioned birds performance (bottom graph) was severely retarded after CP and CT were transected.

In contrast, the sham subject's threshold was indeed minimal and equal to 0.7 mins of arc. Hence it is likely that any effects of the operation *per se* would be detected in this subject's post-operative performance.

The results were quite clear. After DSO or sham operations, neither subjects' threshold was detrimentally effected. In fact, subject 47 actually improved its threshold to a mean of 7.0 mins of arc, despite complete transection of CA and DSO. This improvement indicates that the original estimate of threshold was not minimal. However, after a perfect transection of CP + CT, this subject's performance became unstable and deteriorated rapidly, despite extended post-operative II training. The mean threshold for the first four sessons of post-operative II testing was 21.2 mins of arc, and the mean for all post-operative II sessions was 22.1 mins of arc. Thus the threshold before and after the CP + CT lesion had worsened by a factor of 3. In contrast, the sham operation had no effect on threshold performance. The mean thresholds for the first four sessions of post-operative I and II testing were .9 and .7 mins of arc respectively.

Thus, depth acuity was not affected by transection of the supraoptic decussation, but severely retarded after a complete section through the posterior and tectal commissures.

4.3.4 Monocular Testing

The two sham control birds (67 and 68), both of whom showed no deficit after each surgical session, were strongly affected by the occlusion of one eye. Performance initially dropped to chance and slowly improved over sessions (Figure 4.12). Despite binocular experience on the LACE task, subject 67 required as many trials as

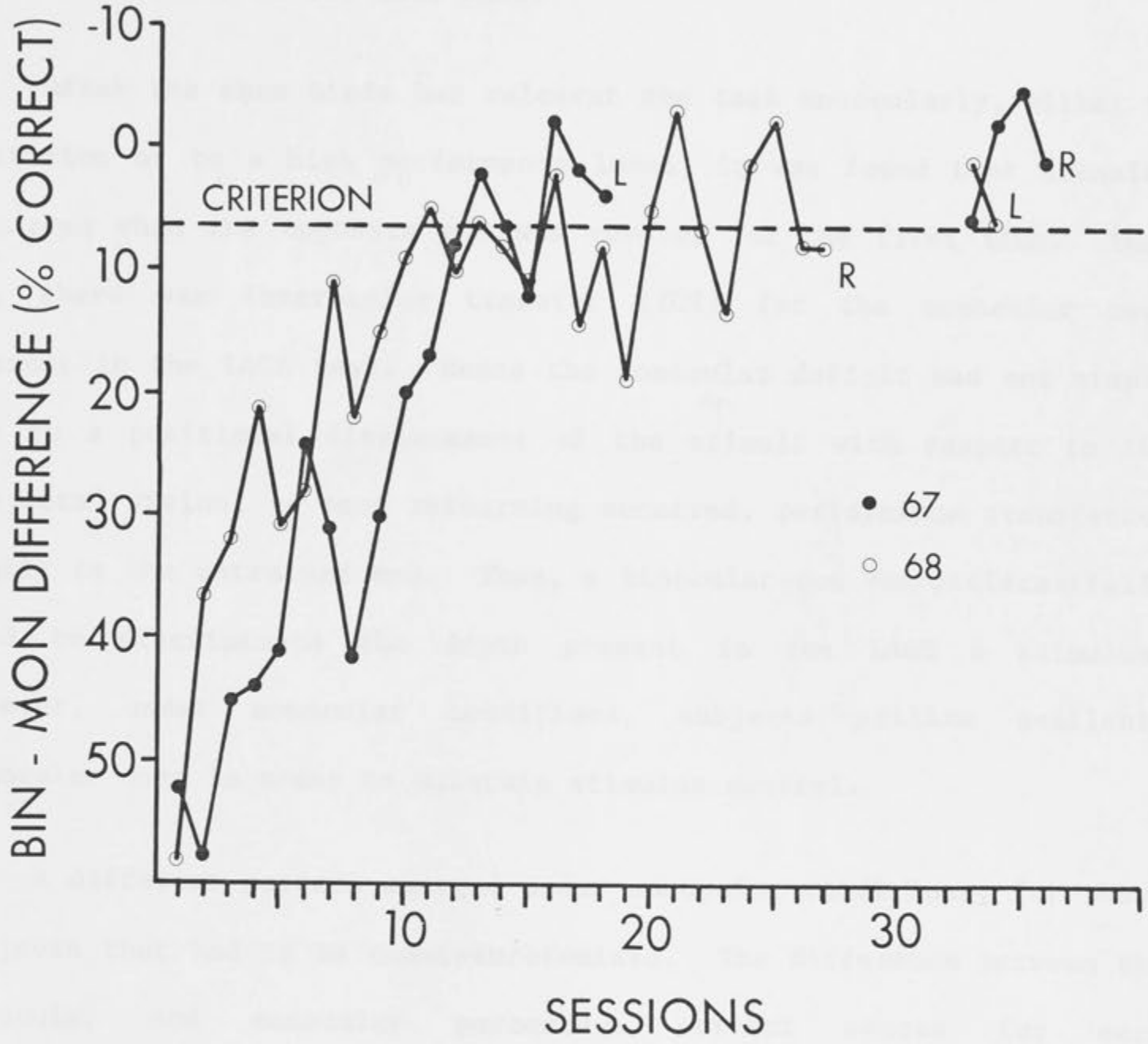


Figure 4.12 The difference between the binocular and monocular percentage correct scores obtained during each session for the sham subjects 67 and 68 trained on the LACE task. Points below criterion indicate a monocular deficit. L, left eye tested; R, right eye tested.

originally taken to relearn the task monocularly, while subject 68 was unable to attain criterion after 28 sessions. In contrast, their binocular performance remained above criterion throughout the testing sessions. Thus the monocular deficit seen on the SDT (Section 2.3.2) was also present on the LACE task.

After the sham birds had relearnt the task monocularly, either to criterion or to a high performance level, it was found that transfer occurred when the opposite eye was covered for the first time. That is, there was interocular transfer (IOT) for the monocular cues present in the LACE task. Hence the monocular deficit was not simply due to a positional displacement of the stimuli with respect to the subjects' vision, as once relearning occurred, performance transferred neatly to the untrained eye. Thus, a binocular cue was preferentially used to discriminate the depth present in the LACE 6 stimulus. However, under monocular conditions, subjects utilize available monocular cues in order to maintain stimulus control.

A different pattern emerged under monocular conditions, for those subjects that had to be commissurotomized. The difference between the binocular and monocular percentage correct scores for each experimental subject tested monocularly, are shown in Figure 4.13. It can be seen that for all subjects that were able to relearn the task after commissurotomy, little deficit occurred when either eye was covered (except in the instance of subject 55)[6].

[6]Subject 55 was unable to discriminate depth with the right eye after repeated sessions. The anatomical results showed extensive necrosis in the left forebrain and the monocular deficit was likely to be a function of this damage in combination with the lack of access to the right hemisphere after commissurotomy. However, no monocular deficit was evident when the left eye was tested as the right forebrain was intact.

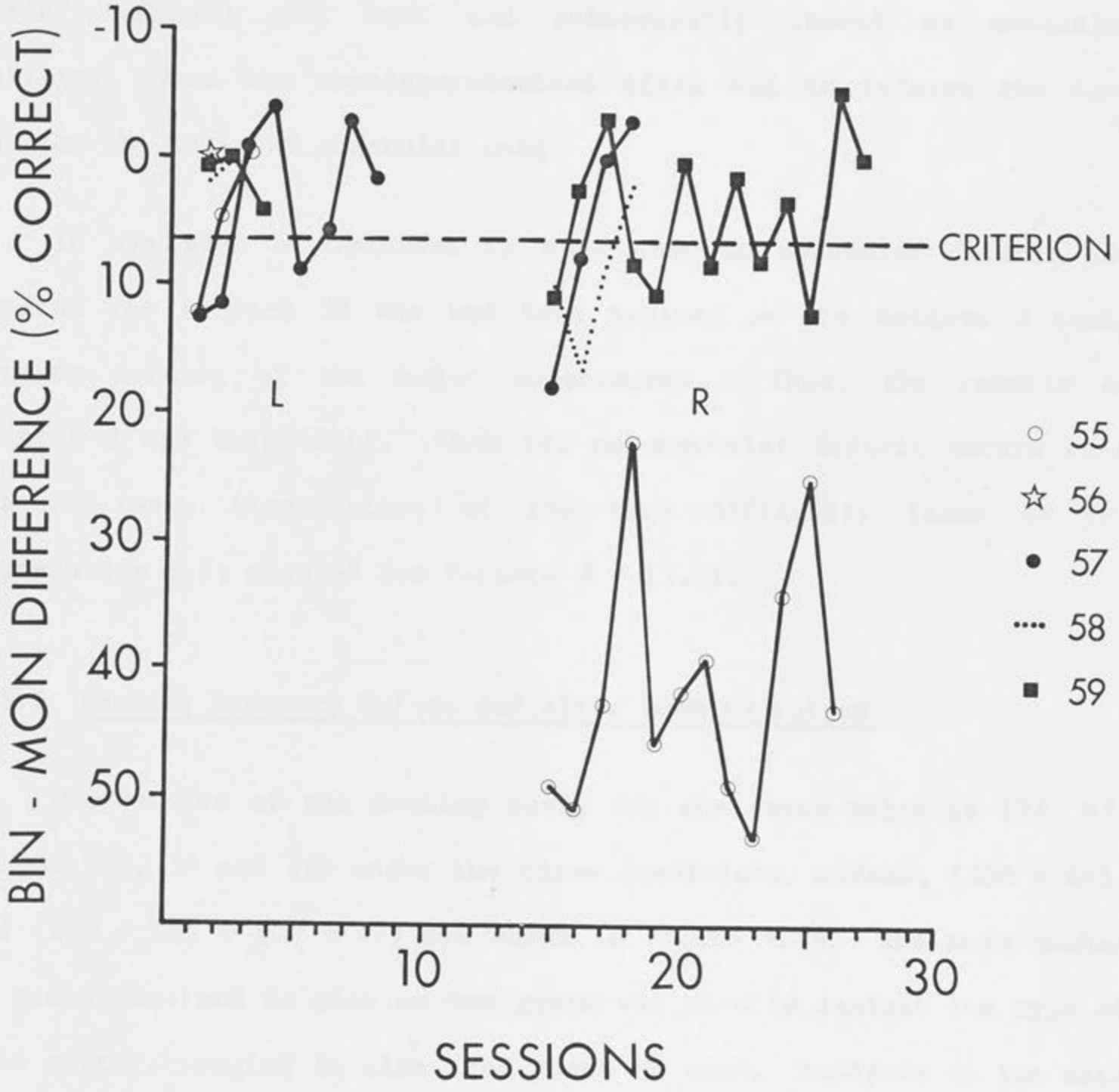


Figure 4.13 The difference between the binocular and monocular percentage correct scores obtained on each session for subjects 55-59. Subject 56 would only respond on the first monocular session. Criterion indicates no monocular deficit. L, left eye tested; R, right eye tested.

The monocular performance of subjects trained on the LACE task and the SDT is consistent with the hypothesis that the behavioural deficits seen after each commissurotomy were due to the loss of the binocular status of the depth task. However, subjects with a 'split-brain' relearnt the task and subsequently showed no monocular deficit. Thus the commissurotomized birds had to relearn the task only on the basis of monocular cues.

It was also of interest to note that no monocular deficit was evident for subject 58 who had been trained on the Pattern 2 task, despite cutting of the major commissures. Thus, the results of Chapter 2 are reinforced. That is, no monocular deficit occurs on a pattern task, irrespective of the task difficulty (mean SN for Pattern 1 = 5.7; mean SN for Pattern 2 = 13.0).

4.3.5 Pecking Accuracy Before and After Commissurotomy

The results of the pecking tests for the seven subjects (37, 47, 55, 56, 57, 58 and 59) under the three conditions: normal, (DSO + CA), and (DSO + CA) + (CP + CT) are shown in Figure 4.14. The mean number of pecks required to pick up one grain was plotted against the type of seed tested, ranging in size from wheat to corn. Analysis of the data using a fixed effect model, randomized block factorial design, revealed that the larger seeds required significantly more pecks than the smaller seeds ($F = 9.8$, $p < .005$, $df = 2,66$). The reason for this difference is not readily apparent. It may be due to the shape of the larger seeds rather than their size.

A strong significant difference was also found between the three conditions ($F = 10.6$, $p < .005$, $df = 3,66$). Inspection of Figure 4.14 shows that the most errors on all seed types were consistently made by subjects after both DSO + CA and CP + CT had been transected. An

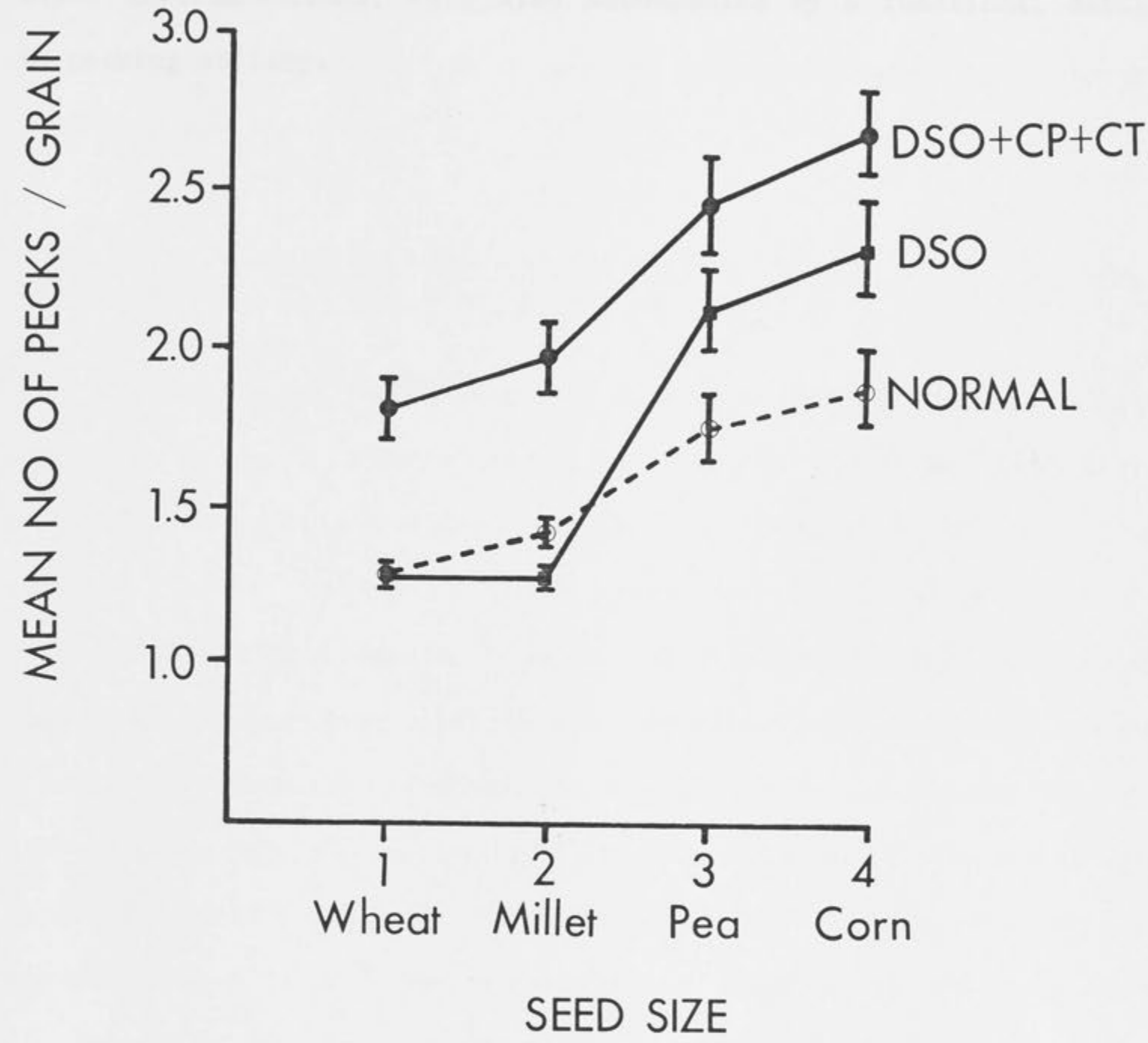


Figure 4.14 Mean number of pecks required to pick up one piece of seed measured for four different types of grain. The error rate was measured in normal birds (○), the same birds after the supraoptic decussation (DSO) and the anterior commissure (CA) were transected (■) and again after the posterior and tectal commissures were cut (●). Bars indicate the standard error.

increase in error rate was also seen for the largest seed size after DSO + CA were transected.[7]

Thus, after both surgical sessions, birds consistently showed more errors in pecking relative to the mean pre-operative performance. Hence, the behavioural deficits noted in the operant depth discriminations, were also accompanied by a functional deficit in pecking ability.

[7] *A posteriori* comparisons (Dunnett, one sided, comparison with normal control) examined the error rate for pecking at the corn. A deficit in pecking was found after both the DSO ($p < .05$) and CP + CT ($p < .01$) had been lesioned when compared with the normal control.

4.4 DISCUSSION

Two main observations result from this chapter. Firstly, progressive commissurotomy produced behavioural deficits on two related depth discriminations. Furthermore, no such deficits were seen on a pattern discrimination. Secondly, the status of the depth discrimination changed from binocular (before surgery) to monocular (after surgery).

4.2.1 The Correlation between the Ventral Aspect of the Supraoptic Decussation and the Binocular Perception of Depth.

Transection of the CA and DSO were found not to affect retention of the pattern 2 discrimination or the SDT However, behavioural deficits occurred on retention of the LACE task after the CA and DSO were sectioned. In the LACE/SHAM group, cutting CA alone had little or no effect on performance. Hence, behavioural deficits on the LACE task were due to transection of the DSO alone. In particular, it was found that behavioural deficits were correlated with damage to DSO_v, thus implicating disruption of input to nuclei of the tectofugal pathway (SP, IPS, T, Rt). It was also found that damage to DSO_d was uncorrelated with performance changes and appeared not to be involved in retention of the depth tasks. This result reinforces the conclusions of chapter 3 - viz - that the visual Wulst was non critical in mediating the binocular perception of depth, since the bilateral projection from the thalamus to the Wulst crosses via DSO_d.

Although small but consistent behavioural deficits occurred on the LACE task as a result of damage to DSO_v, no such effect was seen on the SDT. It is possible that the differential deficits on the two depth related tasks were a function of the fact that the LACE task had significantly longer acquisition curves, making it a more sensitive

test. If this were true, one would expect some effect of DSO transection on the attainment of psychophysical thresholds. Yet here again no deficits were observed. Indeed, the SDT Threshold subject actually improved its acuity after section of the DSO. The possibility remains that a larger sample was needed to detect changes in threshold, particularly considering the poor initial threshold of the one subject tested. Hence it is not clear whether the deficit seen on the LACE task was peculiar to the nature of the depth stimulus. However, retarded monocular acquisition on a variety of colour, pattern and brightness discriminations after section of the DSO in the numerous IOT studies has never been reported (see Burkhalter and Cuenod, 1978).

4.4.2 The Critical Role of the Posterior and Tectal Commissures in Binocular Depth Perception.

In contrast to the puzzling pattern of results after transection of DSO, there was little doubt of the resultant deficit occurring after transection of the CP + CT in addition to the DSO. Performance deficits occurred on all depth related tasks but were not seen at all on retention of the pattern 2 task. These deficits cannot be attributed to the operation *per se*, as little damage was evident in other brain structures and no change in discrimination performance was seen in the sham controls trained and tested on the LACE task.

After transection of the DSO and CA followed by cutting CP + CT (partial split brain), the performance of the subject trained on the SDT thresholds deteriorated rapidly. Depth thresholds became unstable and acuity decreased approximately by a factor of three compared with performance after transection of the DSO and CA alone. In contrast, the sham control maintained a maximal depth acuity throughout the testing procedure.

Behavioural deficits were also seen after partially splitting the brain in subjects trained and tested on the LACE task. Examination of the extent of the knife cuts after testing, revealed that both the tectal and posterior commissures were transected in varying amounts. The emphasis of the lesion was at the anterior aspect, thus encompassing more complete cuts through the CP than CT.

4.4.3 The Change from Binocular to Monocular Vision after Commissurotomy

4.4.3.1 *Relearning the Depth Task after Commissurotomy with only Monocular Cues*

Perhaps the most obvious feature of these behavioural deficits after partial splitting of the brain, is that they were temporary. Relearning occurred during both post-operative testing periods. It is my opinion that this was due to a reduction in the status of the discrimination from binocular to monocular. Thus, subjects with a partial split brain relearned the depth task on the basis of available monocular cues. In support of this hypothesis it was found that when criterion performance was re-attained, occlusion of either eye had little effect on performance levels. This was not the case for the LACE/SHAM birds. These latter birds showed no deficit after each sham operation, but despite their overtraining, were reduced to chance performance when tested monocularly. Without a split brain, these subjects had never been forced to learn the task using monocular cues. Relearning took at least as long as was originally taken to learn the task binocularly. It should also be noted that no such monocular deficit was seen when the commissurotomized pattern 2 bird was tested with one eye occluded[8].

[8]The acquisition rate of the pattern 2 task was similar to the SDT which has already been shown in chapter 2 to also be strongly affected by the occlusion of one eye.

4.4.3.2 *Interocular Transfer of Monocular Cues to Depth*

It was also of interest to find that once the LACE/SHAM birds had learnt the discrimination with one eye occluded, there was complete IOT to the opposite eye. Hence it cannot be argued that covering up one eye simply caused some sort of deficit due to positional displacement. Rather, it would appear that the absence of a monocular deficit after relearning the depth task with a partial split brain was due to effectively changing the depth stimulus from one with salient binocular cues to one relying only on monocular cues.

4.4.3.3 *The Role of Accommodation in Relearning the Depth Task on the Basis of Monocular Cues after Commissurotomy.*

It is suggested in chapter 5 that accommodation was possibly the basis of the monocular discrimination of the LACE depth task. This may explain the retardation in relearning the LACE discrimination after section of the major commissures in addition to a unilateral lesion of the nucleus of Edinger-Westphal (EW). EW is the parasympathetic component of the oculomotor nuclear complex (Lowenstein and Loewenfeld, 1969) and in the pigeon has been described as having three anatomically and functionally distinct subdivisions controlling pupilloconstriction, accommodation and the smooth muscle of the choroid (Reiner *et al.*, 1983).

It was also found that the pupil response in birds that received a lesion to only *one* EW nucleus in combination with the partial split brain, was sluggish in *both* eyes, particularly ipsilateral to the nucleus. With accommodation presumably absent in one eye and possibly affected in the other, it is little wonder the relearning on the basis of monocular cues was so difficult. It is not clear whether accommodation was directly used or was indirectly needed for the adequate use of some other cue. Since criterion performance on the

depth tasks failed to transfer to a simulation of the depth stimuli as viewed from an oblique angle (thus producing possible secondary monocular cues such as object overlay) the notion that the pigeon preferentially uses primary cues to depth receives further support.

4.4.4 The Utilization of Retinal Disparity as a Binocular Cue in the Depth Discrimination

The first main conclusion of this chapter stems from the results that both occlusion of one eye and partial disconnection of the hemispheres results in behavioural deficits on a visual depth discrimination. This implies that the pigeon required the integrated activity of both eyes in order to discern the presence of depth in the positive stimulus.

In chapter 2 it was seen that both relative and absolute convergence could act as the binocular cue to depth in the SDT. The results of the FLIP control in the present chapter can also be explained in these terms (Figure 4.15). Flipping the positive stimulus for the SDT subject resulted in a discriminable change equivalent to that seen in the relative depth task (see Section 2.4.1.2), and performance fell to chance. In terms of absolute convergence angles in Figure 4.15, $\alpha_1 \neq \alpha_2$. This was not the case with the LACE task. The only available binocular cue was that of relative convergence. This can be appreciated when one examines the FLIP control. While flipping the S+ does not change the stimulus (two random arrays of triangles still appear in two planes), flipping S- effectively decreases the absolute convergence angle (see Figure 4.15). Yet subjects were not perturbed by this change, hence indicating that in the LACE task the binocular cue to depth involves the difference between α_1 and α_2 (Figure 4.15b). This is equivalent to the binocular disparity of one point in one plane with

respect to another point in the second plane.

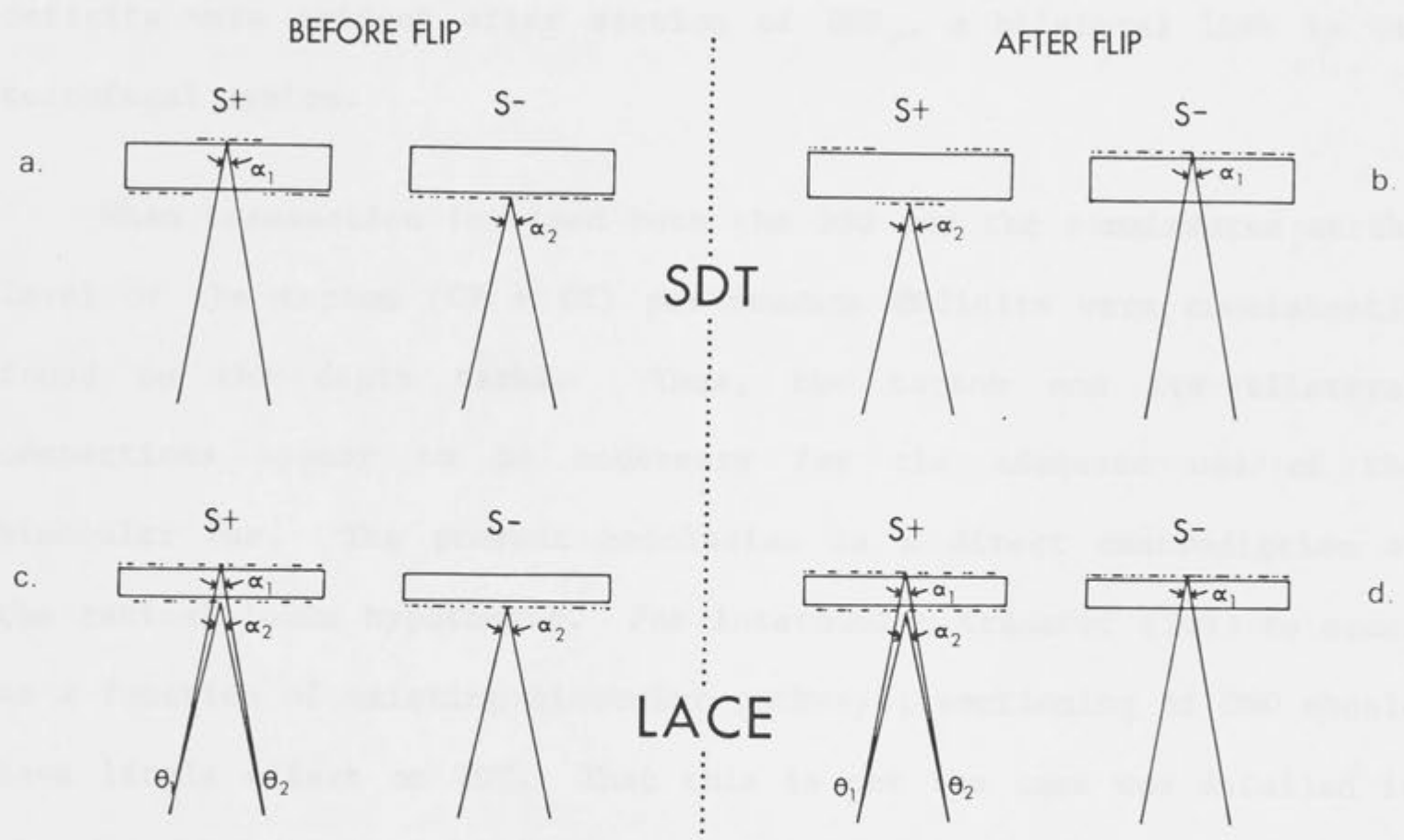


Figure 4.14 a. Absolute convergence can be used as a binocular cue to depth in the SDT providing the subject fixates approximately in the centre of the stimulus, thus α_1 = S+ and α_2 = S-. b. Subjects were unable to respond appropriately when the stimuli were flipped, as the convergence angles associated with S+ and S- were reversed such that α_2 = S+ and α_1 = S-. c. Only relative convergence can be used in the LACE task ($\alpha_2 - \alpha_1 = \theta_R - \theta_L$) since only the absolute convergence angle α_1 = S+ when the stimuli were flipped. d. α_1 would now predict S-. Since subjects still respond to S+ appropriately, α_1 = S+ cannot be the binocular cue.

4.4.5 The Mediation of the Binocular Perception of Depth by the Tectofugal Pathway

The second conclusion of this chapter involves the neural localization of the binocular depth cue. It was found that the major commissure for the thalamo-hyperstrial pathway (DSO_d) was not singularly involved in mediation of the binocular cue. However, deficits were evident after section of DSO_v, a bilateral link in the tectofugal system.

When transection involved both the DSO and the commissures at the level of the tectum (CP + CT) performance deficits were consistently found on the depth tasks. Thus, the tectum and its bilateral connections appear to be necessary for the adequate use of the binocular cue. The present conclusion is a direct contradiction of the retinal locus hypothesis. For interocular transfer (IOT) to occur as a function of existing binocular pathways, sectioning of DSO should have little effect on IOT. That this is not the case was detailed in the introduction to this chapter. There is evidence to suggest a correlation between the proportion of binocular cortical neurones and the degree of IOT in mammals and humans (Sherman, 1971; Movshon *et al.*, 1972; Hohmann and Creutzfeld, 1975; Mitchell *et al.*, 1975). However, here too there are inconsistencies. For example, when visual acuity and eccentric fixation are controlled for, IOT in strabismic patients is normal (Buzzelli, 1981). Good IOT is also present in Siamese cats, which lack the normal contingent of binocular neurons in areas 17 and 18 (Marzi *et al.*, 1976). However the validity of the link between avian and human studies is at this stage tenuous.

4.4.6 The Functional Use of a Binocular Depth Mechanism in Pecking at Grain.

As well as the lesion effects observed on the operant depth discriminations, lesions also produced impairment in the pigeons' ability to peck at pieces of grain. Deficits in pecking were again more pronounced after transection of both the DSO and CP + CT. The question arises as to whether the similarity in behavioural deficits between a particular visually guided behaviour pattern and an operant visual depth discrimination, reflects a motor or a sensory deficit. However, no deficit was seen on a pattern discrimination after similar lesions, suggesting that the deficit was indeed sensory. Both the observations that an experienced one-eyed bird and a pigeon with no functional binocular field, also had problems in pecking at grain similar to those of the split-brain subjects, (McFadden, personal observations) leads to the conclusion that the observed impairments were due to a change in the animals' sensory capacity.

As the pigeon is widely believed to be relatively myopic in its anterior binocular field (Catania, 1964; Nye, 1973), the functional use of a binocular depth mechanism is presumably limited to near vision. It has long been suggested that the binocular 'red-area' may be primarily involved in the control of pecking in the pigeon, providing information about the location and distance of objects in front of the beak (Nye, 1973; Clarke and Whitteridge, 1976b; Goodale and Graves, 1982; Goodale, 1983a). Data in this thesis strongly suggests that the judgement of the depth of stimuli within the binocular field is provided by a binocular depth mechanism which is capable of comparing the relative angles of convergence of one point with respect to another.

CHAPTER FIVE

GEOMETRICAL DETERMINATION OF THE BINOCULAR FIELD AND VIEWING DISTANCE OF THE PIGEON DURING DISCRIMINATION PERFORMANCE.

CONTENTS

5.1 SYNOPSIS

In order to determine the position of the stimuli with respect to the binocular field of the pigeon it was necessary to make two measurements. The first was the absolute size and position of the binocular field. The second was the distance from the centre of the pupils to the stimulus during the discrimination performance. The latter measurements were also needed to determine the threshold retinal disparity values given previously in chapter 3. Photographic analysis of the bird's behaviour during discrimination performance was analysed, not only under normal binocular conditions, but also during monocular sessions.

5A. THE EXTENT OF THE RETINAL BINOCULAR FIELD

5.2 INTRODUCTION

Panoramic vision in the pigeon extends 340° (Walls, 1942). It is achieved by the large monocular visual fields (each estimated 180°, see Chard and Gundlach, 1938), and by the lateral placement of the two eyes whose optical axes form an angle of approximately 145° (see Donovan, 1978). Although not allowing for refraction in the cornea, the divergence of the optic axes has been used as a crude index of the width of the binocular field (Johnson, 1901; Walls, 1942, pp. 291-298), and in the pigeon allows some 24° of overlap (Chard and Gundlach, 1938; Walls, 1942) (see Figure 2.1).

In measuring the binocular field of the pigeon, various methods have produced disagreement about the precise extent and position of the field. Martinoya *et al.* (1981) photographed pigeons from different visual field directions and analysed the shape of the pupils' images. They define the elevation at which the maximum binocular field width occurs, as the intersection of the sagittal plane containing both optical axes. Both the point at which the long axes of the ovoid shaped apparent pupils were parallel and the direction for which the product of the width of both apparent pupils was maximal, indicated that the widest portion of the binocular field was inclined 23° *below* the eye-beak axis. In this direction the width of the absolute binocular window was about 40° and extended 110° in height.

While Martinoya *et al.* (1981) describe the optical cyclopean binocular field, Martin and Young (1983) measured the retinal binocular field using the ophthalmoscopic reflex technique (Hughes, 1979). In disagreement with the previous study, Martin and Young

locate the region of maximum binocularity at 20° *above* the eye-beak axis. In addition, they found that the vertical extent of the binocular field was 130° and extended 90° above and 40° below the eye-beak axis. The maximal width of the field was 28°.

The clear discrepancy between the two studies cannot be simply attributed to the difference between the optical and retinal fields, since Martin and Young (1983) also report that the elevation at which maximum retinal and optical binocularity occurs, are at similar loci. As pupil diameter is unlikely to account for the discrepancies in the vertical locus of maximum binocular field width, it would appear that the differences may in fact be due to the different breeds of pigeon used. Martinoya *et al.* (1981) used the Corneau Rouge breed while Martin and Young (1983) used the English Racing Homer pigeon. Given these discrepancies, it was necessary to measure the retinal binocular field of the feral pigeons used in this thesis. The method used was similar to that described by Martin and Young (1983), although simplified by the use of a reversible ophthalmoscope. This device had a corner cube which allowed back projection of incident light by 180°.

It would be expected that the binocular field was directed at the stimuli during visual discrimination performance. Clearly, this would be necessary in order to use binocular cues in the depth discrimination. However, not all birds were able to learn the depth discriminations. It was noted in Section 2.3.1.2 that 11% of the sample were unable to accomplish the SDT. It was possible that these birds either did not direct their binocular fields at the stimulus or that something was amiss with their binocular fields. The binocular fields of two such 'non-learners' were measured, and it was indeed found that these birds had abnormal binocular fields.

5.3 METHODS

5.3.1 Subjects and Preparations

Six pigeons were used. Four were normal naive birds (subjects numbers 80-83). The remaining two subjects (66, 54) had both been trained behaviourally and had been unable to learn the SDT after extended training. The birds were anaesthetised with Ketamine in combination with Xylazine as described in Section 3.2.4.1. Little muscle tonus was apparent and eye movements appeared absent for approximately 30 minutes. The eye lids were partially retracted and held back with tape.

5.3.2 Procedure

Retinal binocular fields were measured by mapping the reflex from the retina (Hughes, 1979) with a reversible ophthalmoscope. The sedated birds were mounted in a modified stereotaxic apparatus that enabled unimpeded viewing of the eyes through the ophthalmoscope. This was achieved by supporting the bird's head via the ear bars and replacing the beak bar with a ring that fitted neatly around the entire beak, directly below the nostrils. The ring was mounted from a rod that ran flush with the underside of the neck. The stereotaxic apparatus was mounted on an adjustable coupling such that the bird's head could be positioned in a variety of directions.

The bird was aligned so that the lower straight edge of the upper mandible immediately below the cere, was normal to a tangent screen placed approximately 80cm in front of the pigeon (Figure 5.1). In order to be compatible with previous measurements, the anterio-posterior (AP) zero plane was taken through the centre of the pupils and parallel to the lower straight edge of the upper mandible.

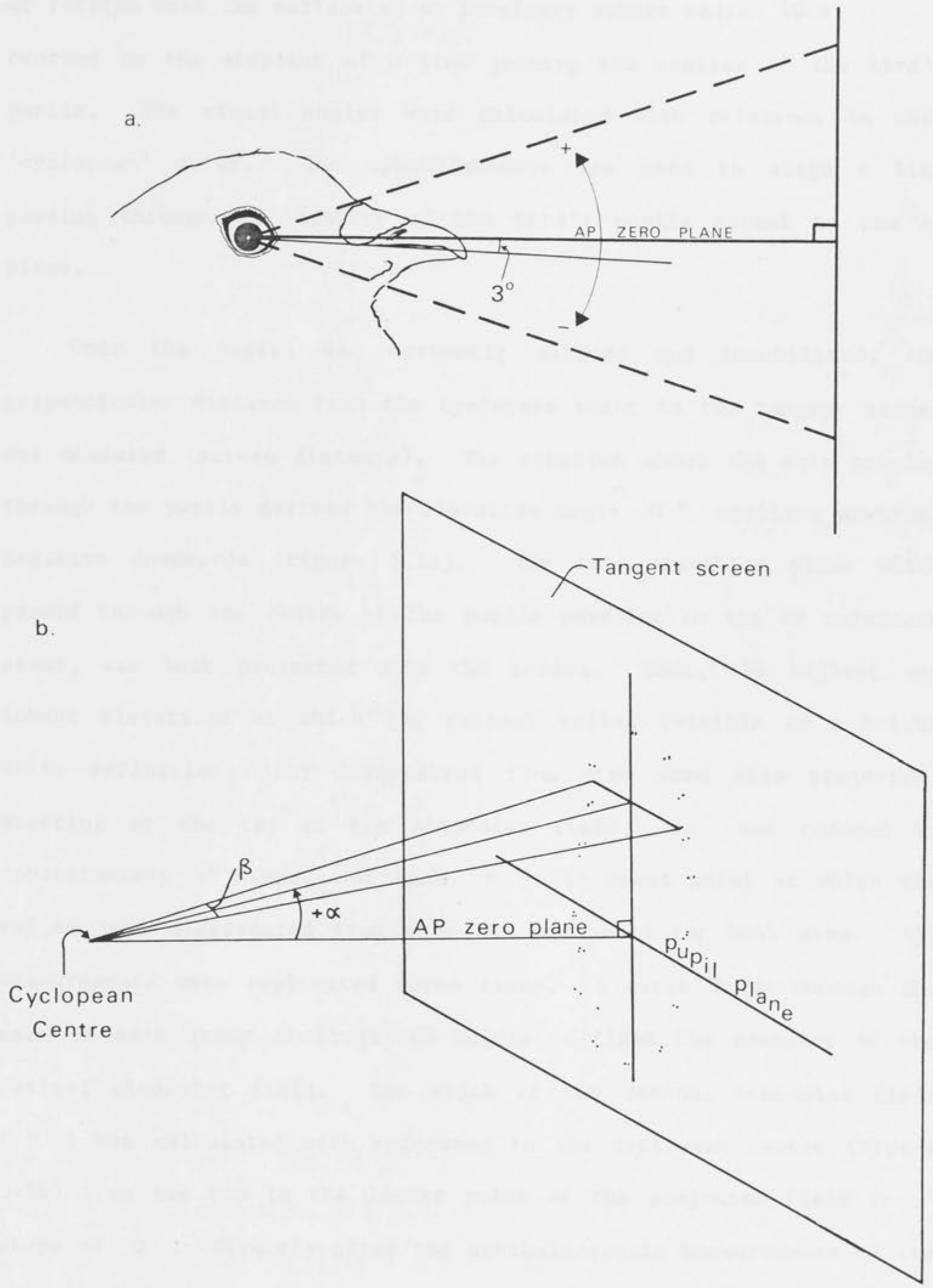


Figure 5.1 a. Alignment of the bird's head to the tangent screen. The anterio-posterior (AP) zero plane lies 3° above a line drawn through the last point on the straight edge of the upper mandible and the centre of the pupil, b. Parameters of the binocular field in relation to the cyclopean centre, β is the binocular field width for a particular elevation angle α .

The ophthalmoscope was mounted on a flexible arm that could be clamped or rotated over the surface of an imaginery sphere radius 40cm centred on the midpoint of a line joining the centres of the bird's pupils. The visual angles were calculated with reference to this 'cyclopean' point. The ophthalmoscope was used to align a line passing through the centres of the bird's pupils normal to the AP plane.

Once the pigeon was correctly aligned and immobilized, the perpendicular distance from the cyclopean point to the tangent screen was measured (screen distance). The rotation about the axis passing through the pupils defined the elevation angle α °, positive upwards, negative downwards (Figure 5.1a). The zero elevation plane which passed through the centre of the pupils parallel to the AP reference plane, was back projected onto the screen. Next, the highest and lowest elevations at which the retinal reflex (visible as a bright white reflection) just disappeared from view were also projected. Starting at the top of the binocular field, α was reduced in approximately 5° steps. At each α , the nasal point at which the reflex just disappeared from view was projected for both eyes. All measurements were replicated three times. A curve drawn through the mean of each group of projected points, defined the boundary of the retinal binocular field. The width of the retinal binocular field (β °) was calculated with reference to the cyclopean centre (Figure 5.1b) from the top to the lowest point of the projected field in 5° steps of α . Directly after the ophthalmoscopic measurements of the extent of the retinal binocular field were completed, the projections of both foveas were noted (visible as a light blue concentric light reflex) and the angle between the foveas was calculated.

5.4 RESULTS

5.4.1 Binocular field of normal birds 80-83

The binocular fields of subjects 80-83 were generally symmetrical about the zero plane. The mean vertical extent of the retinal binocular field was 83° (σ_{n-1} = 8°) with a maximum width of 24° (σ_{n-1} = 5.7°) occurring within ± 5° of the zero plane. A representation of the mean curve for subjects 80-83 is shown in Figure 5.2. Each individual's binocular field width (β) plotted as a function of the elevation angle (α) is shown graphically in Figure 5.3. The details of maximum width, total elevation above and below the zero plane and foveal angles (angle between the visual axes) for each bird is tabulated in Table 5.1

The beak and cere did not interfere with the projection of the light reflex since the ophthalmoscope was placed 50cm from the cyclopean centre, rather than close to the eye. The position of the foveas were noted by close examination of the eye with the ophthalmoscope and the mean foveal angle for all birds was 135° (σ_{n-1} = 3°).

5.4.2 Binocular field of birds which were unable to learn the SDT

Both subjects (66 and 54) who were unable to learn the behavioural depth discrimination had abnormal binocular fields. Subject 54 has no functional binocular field. It was limited entirely by a large build-up of cere under the eyes and on the beak. Subject 66 had a reduced binocular field that was about half the mean field of the normal subjects in both maximum width (β_{max} = 9.8° at α = -5°) and vertical extent (Max α = 10.7°, Min α = 32.2°, Total α = 42.9°). The graph showing the binocular fields of the

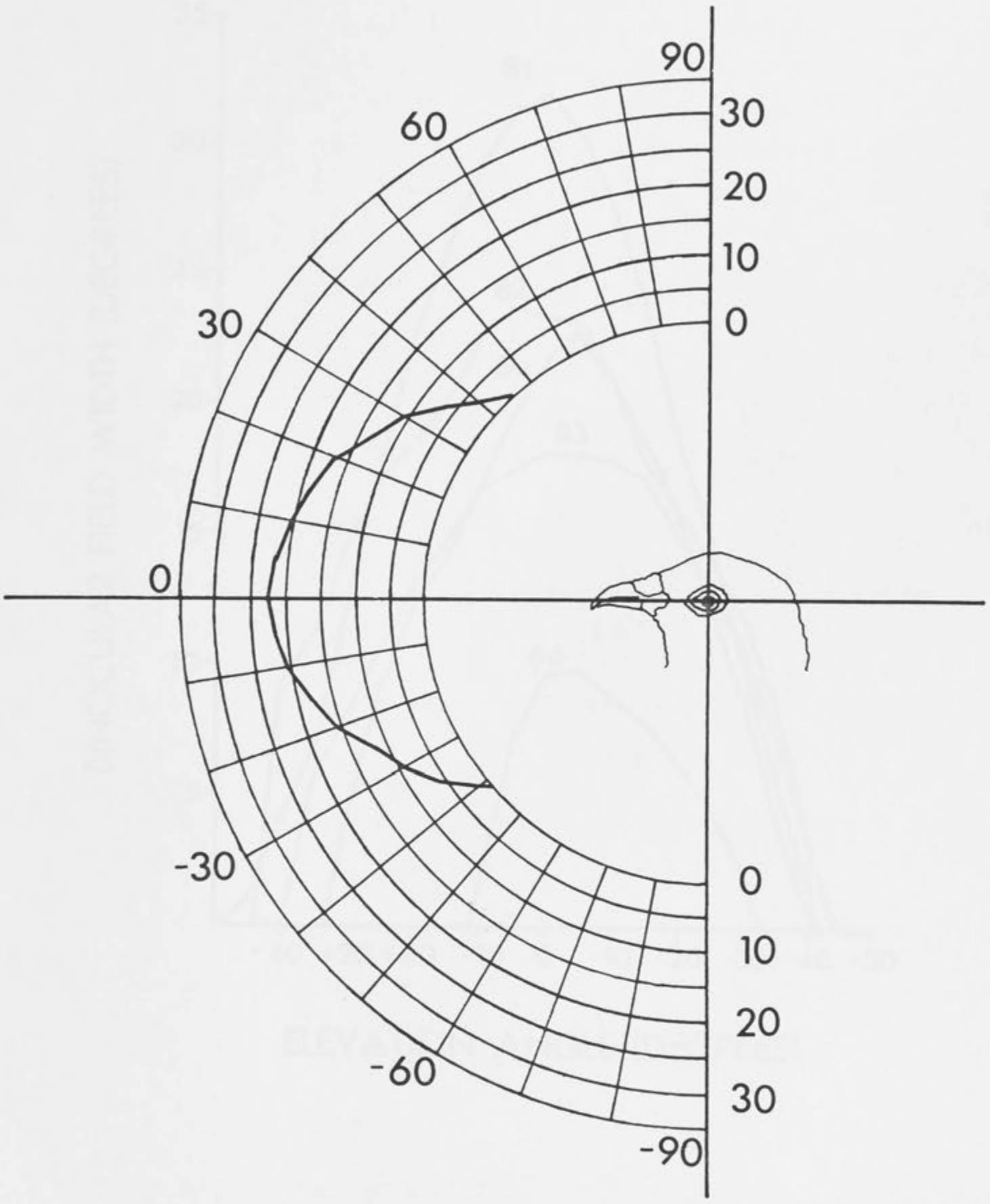


Figure 5.2 The mean retinal binocular field for subjects 80-83. The vertical axis indicates the binocular field width β °. The circular axis represents the elevation angle α °, $+\alpha$ is above the AP plane, $-\alpha$ is below the AP plane.

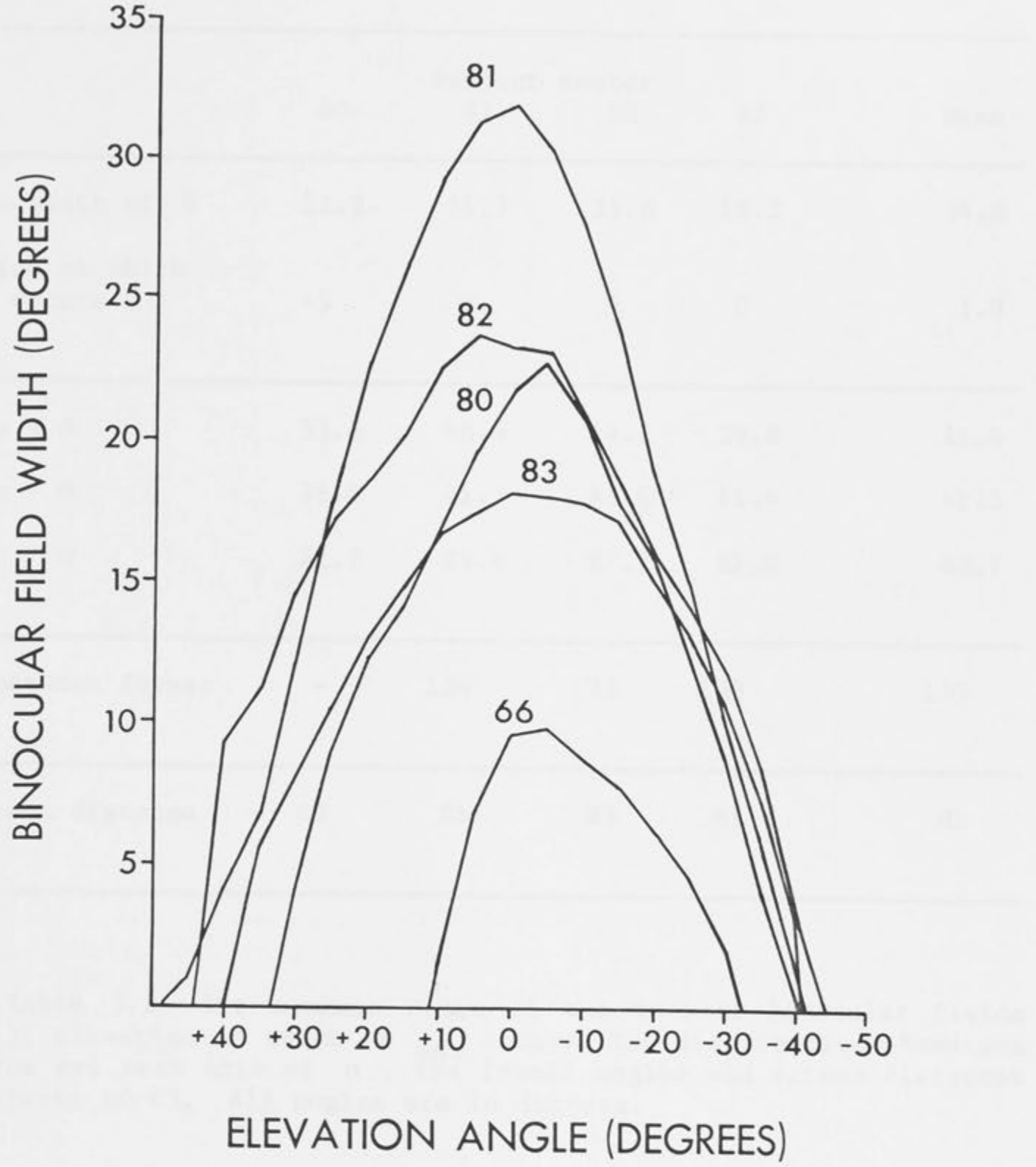


Figure 5.3 Retinal binocular fields of individual birds plotted as a function of the width of the field (β °) and the elevation angle (α °). Subject 66 had an abnormal binocular field.

normal subjects 80-83 also includes the projection found for subject 66 (Figure 5.3).

	Subject number				
	80	81	82	83	Mean
Maximum width of β	22.2	31.7	23.6	18.2	24.0
Elevation at which β_{max} occurs	-5	5	5	0	1.3
Maximum + α	33.4	48.5	44.1	39.8	41.4
Maximum - α	38.8	41.3	43.6	41.4	41.3
Total α	72.2	89.8	87.7	81.2	82.7
Angle between foveas	-	134	133	139	135
Eye-screen distance	80	81	83	81	81

Table 5.1 The maximum width of the retinal binocular fields (β_{max}), elevation at which β_{max} occurs, the distribution above and below the eye beak axis of α, the foveal angles and screen distances for subjects 80-83. All angles are in degrees.

A comparison of the position of the boundaries of the uniocular fields of subject 54, and the binocular field of subject 66 with the mean normal binocular field is shown on an equatorial orthographic projection in Figure 5.4. The advantage of this projection is that the angular width of the binocular field at all elevations in front of the bird can be read directly from the projection and there is little distortion of field shape about the median sagittal plane.

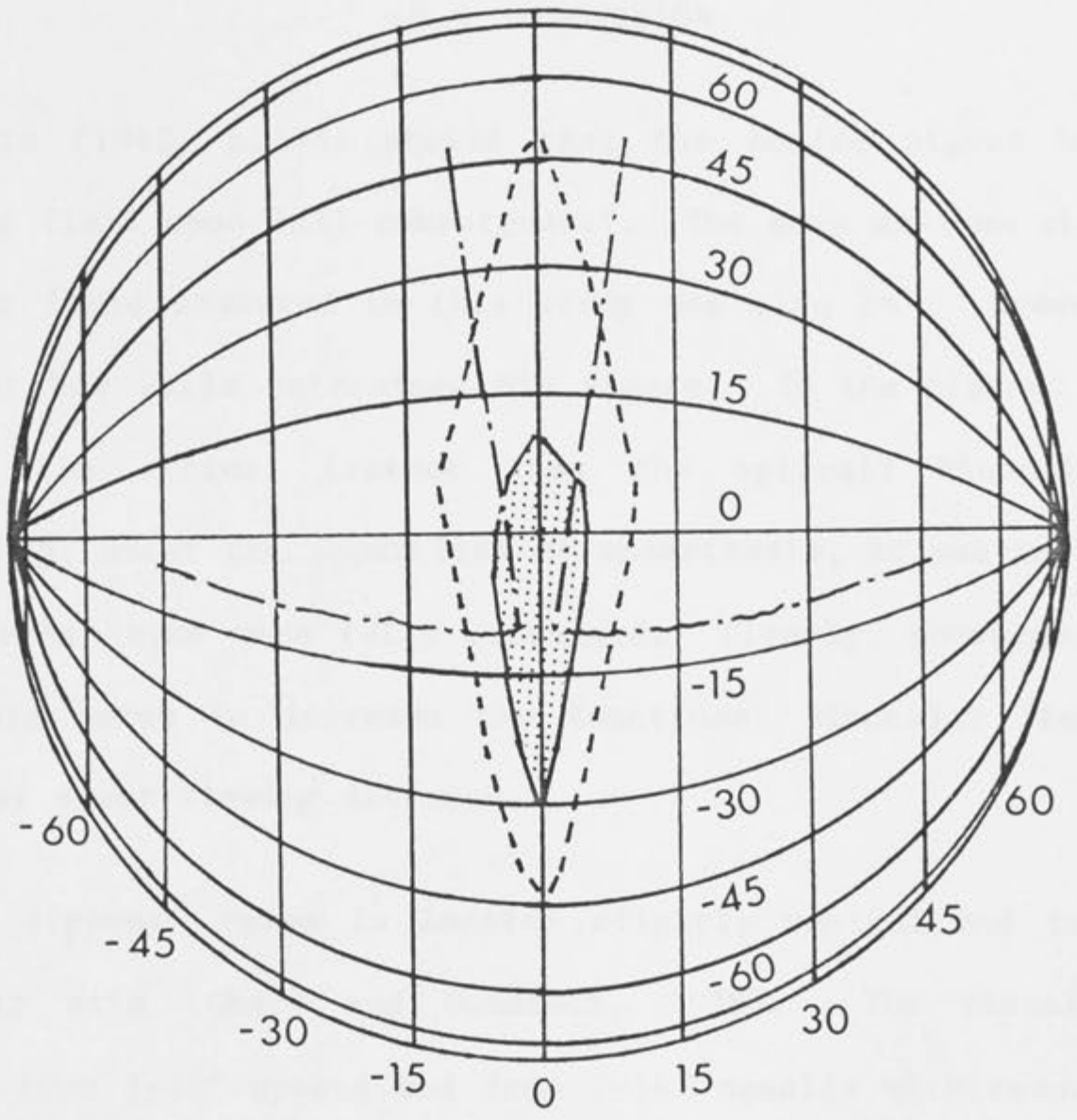


Figure 5.4 Comparative equatorial orthographic projections of the mean retinal binocular field of normal subjects (---), the reduced binocular field of subject 66 ▨, and the uniocular boundaries in subject 54 who had no binocular field (— - —). Subject 54 was blind in the frontal and lower visual field. In this projection the AP zero plane is normal to the plane of the page and passes horizontally through the centre of the projection (0,0).

In Figure 5.4, the medial edges of the uniocular visual fields for subject 54 were mapped up to 50° above the zero plane. The nasal boundaries did not overlap and the subject was effectively blind in the frontal visual field. No visual field was evident approximately 10° below the zero plane. Subject 66 did have some binocular field, and although small, the shape of the field was similar to the normal subjects in that it was ovoid with a maximum diameter occurring near the zero plane ($\alpha = -5°$).

5.5 DISCUSSION

Walls (1942, p.295) stated that the homing pigeon has a '24° binocular field upon full convergence'. The mean maximum width of the binocular field measured in this study was also 24°. However, it is not clear how Walls determined his figure. In the present study, we measured the retinal (rather than the optical) binocular field. Furthermore, under the conditions of anaesthesia, it was unlikely that the subjects' eyes were fully converged. Clearly, convergence of the eyes would serve to increase the functional binocular field of the pigeon for a set viewing distance.

The pigeons' fovea is located slightly ventral and temporal to the optic axis (Chard and Gundlach, 1938). The visual axis is inclined from 5-10° upward and from 7-14° nasally with respect to the optical axis (see Donovan, 1978). Since the angle between the optical axes has been estimated at 145° (see Donovan, 1978), a rough estimate of the angle between the lateral visual axes is 131°. Hence, the 135° reported in this study (Table 5.1) indicates that the Ketamine anaesthetic only caused the eyes to diverge slightly. Cooper and Pettigrew (1979) have also noted that Ketamine had little effect on eye position in the owl. Given the angle between the visual axes, it can also be calculated from optical first principles that under the conditions of anaesthesia in the present study , each eye had diverged by approximately 3°. This geometrical calculation was based upon the schematic pigeon eye described by Marshall *et al* (1973) and the retinal flat mount detailed by Binggeli and Paule (1969). Thus, the binocular field widths reported here slightly underestimate the natural binocular field for a hypothetical infinite viewing distance.

The retinal binocular fields reported in this study were symmetrical about the zero plane. This configuration differs from both the optical and retinal binocular fields reported by Martinoya *et al.* (1981) and Martin and Young (1983). A comparison of these studies with the present results is shown in Figure 5.5 on an equatorial orthographic projection.

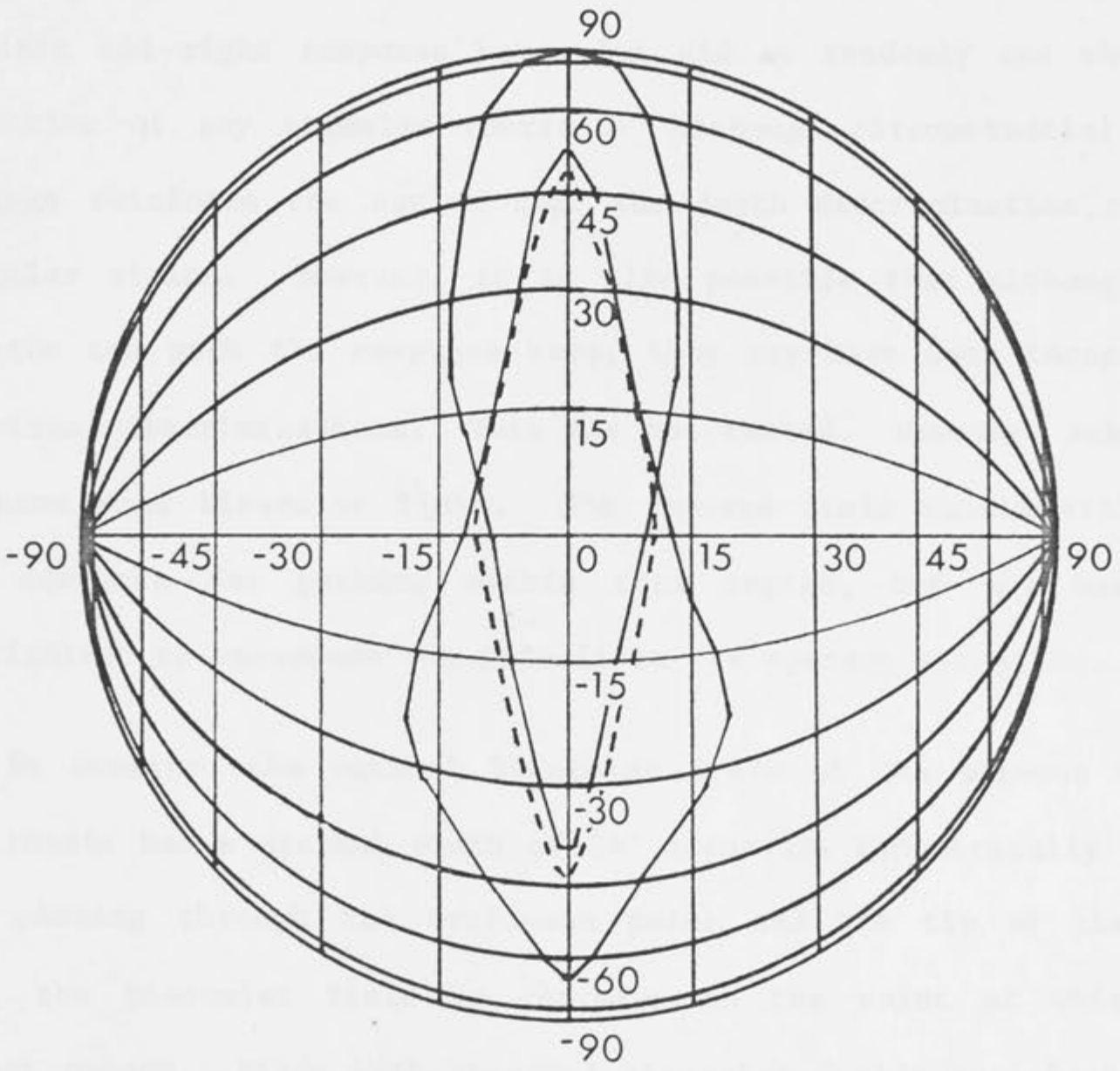


Figure 5.5 A comparison of the retinal binocular field found in this study (---) with the binocular fields reported by Martinoya *et al.* (1981) (upper projection) and Martin and Young (1983) (lower projection). Notice that the widest part of the field differs radically in the three cases. The present study coincides with the intersection of the other sets of data.

It was of interest to find that the mean retinal binocular field reported here coincides with the intersection of the two other sets of data. The significance of this result is not clear, and may only reflect differences between head structure of the various breeds of pigeon. The retinal binocular field found in this study (Section 5A) will be used in estimating the stimulus value in the following study (Section 5B).

It was also of interest to find that those subjects that had abnormal binocular fields, or no binocular field, were unable to learn the depth discrimination. These subjects were capable of pecking both the left and right response keys, but did so randomly and showed no indication of any stimulus control. Although circumstantial, these findings reinforce the notion that the depth discrimination requires binocular vision. However, it is also possible that although these subjects can peck the response keys, they may have been incapable of any visual discriminations. This was not tested. However, subject 66 did have some binocular field. The reduced field should still have been adequate for pecking within this region, but may have been insufficient to encompass the stimuli in the operant situation.

In summary, the retinal binocular field of the pigeons used in this thesis has a maximal width of 24° occurring symmetrically about a line passing through the cyclopean point and the tip of the beak. Thus, the binocular field is centered on the point at which peck contact occurs. Birds with abnormal binocular fields were found to be unable to learn a visual depth discrimination. Whether the maximum width of the binocular field directly corresponds to the specialised region in the upper temporal quadrant of the retina characterized by a high tectal magnification factor, a ganglion cell density comparable to that of the central fovea in the monocular field, and a 'red-area'

in which many of the cones contain red oil droplets, remains to be determined. However, many authors have speculated that the two coincide (Whitteridge, 1965; Galifret, 1968; Binggeli and Paule, 1969; Yazulla, 1974; Clarke and Whitteridge, 1976b; Goodale, 1983a, b). This question will be further discussed in Section 6.1.

5B. VISUALLY GUIDED PECKING DURING OPERANT DISCRIMINATION AND THE POSITION OF THE BINOCULAR FIELD.

5.6 INTRODUCTION

In order to determine the visual depth acuity of the pigeon in terms of retinal angle, it was necessary to know the distance of the stimulus from the anterior nodal points of the eyes. Hodos *et al.* (1976) used high speed cinematographic analysis of the head location of the pigeon during the discrimination of square wave gratings in order to calculate near-field visual acuity. In support of a previous observation (Smith, 1974) they found that the pigeons always closed their eyes and opened the beak shortly before contact with the key. Hodos *et al.* (1976) calculated the point at the beginning of each peck sequence, at which the eye was still fully opened, to be 52mm (between the anterior surface of the cornea and the surface of the key). This estimate was subsequently used in calculating the visual acuity, as most of the inspection appeared to take place at this point.

In a more detailed analysis of the pecking sequence of the pigeon, Goodale (1983a) found that the sequence of behaviour shown by pigeons pecking a key in a feature-positive task was extremely stereotyped. As Jenkins and Sainsbury (1970) observed in their original study of the feature-positive task, the pecks themselves were always directed at the dot, no matter where on the key it was located. Goodale noted that two distinct head fixations occurred shortly before pecking the dot. He referred to these fixations or 'F-stops' as F1 occurring 82mm from the key, and F2 occurring only 55mm from the key. By also examining negative trials and temporal parameters of the F-stops, it appeared that the decision to peck occurred at F1.

In addition, Goodale found that in line with the close resemblance between pecking at keys and pecking at grain noted by other authors (Wolin, 1948; Moore, 1973; Smith, 1974; Zeigler *et al.*, 1980) pigeons also displayed two stereotyped head fixations while pecking vertically at grain. The second F-stop (F2) occurred at the same position as in the key-pecking situation. F1 however, occurred at a greater distance in the free feeding situation than in the key-pecking task by some 15mm. Again, the evidence suggested that the decision to initiate a pecking sequence was made at F1. It appeared that the selection of a feeding area was made from F1, and then a rapid series of accurate pecks was initiated from the F2 position. Goodale claims that information about the location, size and distance of particular seeds was obtained during F2 since the the peck response from F2 is largely ballistic (Zeigler *et al.* 1980; Levine and Zeigler, 1981).

The position of the F2 fixation described by Goodale, is the same in both a key-pecking task and in normal feeding behaviour, and also corresponds to the initial fixation point ('far-point') calculated by Hodos *et al.* (1976). However, if Goodale is correct in saying that the decision to initiate a pecking sequence was made not at F2, but nearly 30mm further back from the key at F1, then current estimates of the visual acuity of the pigeon, would be increased by 35%. Clearly it is necessary to determine the position of head fixations for individual experimental paradigms, as it is not clear whether variation in F2 shown between Goodale's two tasks was due to the size of the stimulus or some other variable.

In addition to measuring the position of head fixations, Goodale (1983) also measured the viewing angles of the birds at both F-stops. He found that in the key-pecking task, the position of the dot

on the positive stimulus with respect to the eye, did not differ significantly from the eye-beak axis (see Figure 5.6). Similar results were found for the grain feeding situation, although the seed at which the bird was pecking could not be accurately located in the analysis. The birds Goodale used were White Carneaux pigeons, the binocular field of which has not been accurately measured. Nevertheless, the binocular field width measured in part A were maximal at the AP zero plane, and it is highly probable that the pecking targets were located directly within the binocular field.

In order to ascertain the position and extent of head fixations in the experimental paradigms used in this thesis, photographic analysis of pecking was undertaken to provide a measure of the eye to key distance. This value allowed the accurate calculation of the visual depth acuity. In addition, the precise location of the binocular field could be projected onto the stimulus. Furthermore, it was of interest to observe the pigeons' behaviour on the depth task during monocular viewing conditions to allow insight into the basis of possible monocular cues.

5.7 METHODS

5.7.1 Subjects

Ten pigeons were used in the following studies, all of which were previously trained to criterion[9] on a behavioural discrimination as indicated in Table 5.2. All subjects were trained as described in Section 2.2.4.

Group		Behavioural Discrimination	Identification Number of Subject
1		Pattern 2	58, 59
2	A	SDT	56
	B	SDT/Thresholds	47
3	A	LACE/Binocular	48, 55, 57, 59, 67, 68
	B	LACE/Monocular	67, 68

Table 5.2 Identification numbers of subjects filmed during various behavioural tasks. All subjects were trained on their indicated task according to the methods described in Section 2.2.4. For a description of the LACE task see Section 4.2.2. SDT is the standard depth task. The stimuli used in each group are described below in Section 5.7.3.

5.7.2 General Procedure

The performance of each bird while key pecking was filmed at 50 frames/second (transistorized TV camera with 55mm Minolta lens

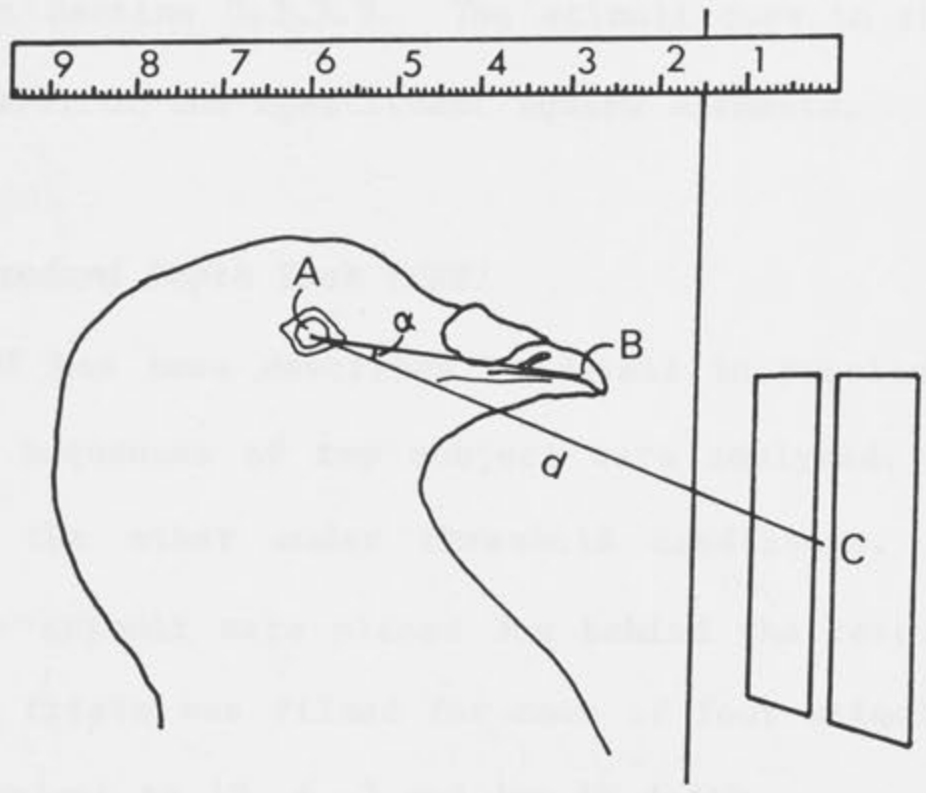
[9]In the case of subjects 67 and 68 who performed a behavioural discrimination under monocular conditions, criterion performance was attained when subjects were highly trained and scored approximately 80% correct.

attached) and recorded on a video system (National VTR NV-3020) for analysis. The camera was in a dark room on the outside of the one-way glass insert of the operant chamber described in Section 2.2.2. A direct side view of the pigeon was obtained together with a millimeter scale running normal to, above, and centered between the two response keys, parallel to the ceiling of the chamber (Figure 5.6a). The video frames were superimposed on a centimeter grid calibrated from the millimeter scale discernible in each frame. Thus, subsequent measurements could be made of the distance from the centre of the closest pupil (right eye) to the centre of the bar between the two response keys. This distance (d) will be referred to as the *eye-key* distance.

The visual *viewing angle* (α) between a line drawn between the last point on the straight part of the lower edge of the upper beak and the centre of the pupil, and the centre of the bar between the two response keys (see Figure 5.6) was also noted for each frame analysed. If the eye-beak line fell above the eye-key axis, α was defined as negative. The viewing angle was termed positive for cases in which the reverse was true (Figure 5.6b). A viewing angle of zero was only encountered when the eye-beak line was coincident with the eye-key axis.

After a subject had reached criterion on its particular task, one full session (96 trials) was recorded on the video system. Approximately 20 correct peck sequences were analysed frame by frame for each of the following behavioural manipulations. There were very few incorrect sequences as subjects were highly trained and rarely made errors. These were not analysed.

a.



b.

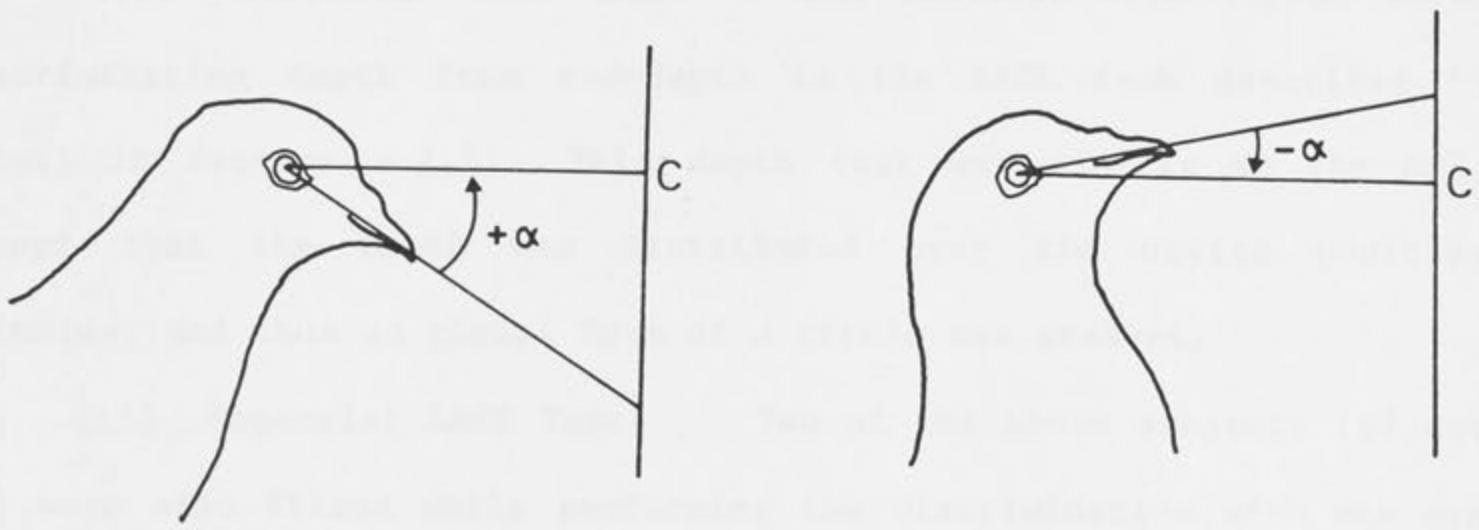


Figure 5.6 a. Typical image obtained in each frame showing the position of the millimeter scale, the distance, d, between the centre of the pupil (A) and the centre of the pecking keys (C), and the visual viewing angle α between the eye-beak axis (AB) and the eye-key axis (AC); b. illustration of the positive and negative viewing angle.

5.7.3 Behavioural manipulations

5.7.3.1 *Pattern 2*

Two subjects were trained to criterion on the pattern 2 task described in Section 3.2.3.2. The stimuli cues in this task were the size and number of the constituent square elements.

5.7.3.2 *Standard Depth Task (SDT)*

The SDT has been described in detail in previous chapters. The behavioural sequences of two subjecs were analysed, one under normal conditions, the other under threshold conditions. For the latter subject, the stimuli were placed 3cm behind the response keys and one block of 24 trials was filmed for each of four stimulus sets in which S+ was equivalent to 10, 6, 3 and 1mm in depth.

5.7.3.3 *LACE Task*

(i) Binocular LACE Task: Six subjects were filmed while discriminating depth from non-depth in the LACE task described in detail in Section 4.2.2. This depth task was similar to the SDT, except that the depth was distributed over the entire positive stimulus, and thus no global form of a circle was present.

(ii) Monocular LACE Task: Two of the above subjects (67 and 68) were also filmed while performing the discrimination with one eye covered. The left eye was occluded in subject 68, while the right eye was occluded in subject 67. Scores of 79% and 83% were achieved during the session for 67 and 68 respectively. Independent analysis was done for trials in which the correct key was on the blinded side or the non-occluded side of the bird. For subject 67, the centre of the pupil was taken as the centre of the goggle marked by a white dot.

5.8 RESULTS

All subjects began a response sequence immediately after the onset of the houselight and keylights at the beginning of each trial. A number of distinct head fixations occurred prior to emitting the final peck, each preceded by a rapid saccade-like movement of the head. During this rapid movement, the subject appeared slightly blurred. Temporal measures of the fixations were not noted although a fixation generally occurred over 4-8 frames (80-160ms) and appeared to be shortest for the final fixation.

5.8.1 Pattern 2

Both subjects made two head fixations (F1 and F2) between the commencement of the trial and the emission of the final peck. The mean eye-key distance was 7.0cm for F1 and 3.8cm for F2. Details for each bird are displayed in Table 5.3.

During fixations, the bird was always positioned with the beak pointing directly at the response keys. The head was never positioned for best monocular viewing. The centre of the bird's head at F1 was always aligned approximately midway between the two response keys and the pigeons' mean viewing angle was approximately zero. The subject then repositioned itself so that it was directly in front of one of the two response keys (F2) and the eye-beak axis fell 10° above the eye-key axis. At both F1 and F2 the widest part of the binocular field was thus directed at the keys. A peck was always initiated from F2 and the subject had its eyes closed and beak open at the point of contact with the key.

Subject		Eye-key distance (cm)		Viewing Angle (α °)	
		F1	F2	F1	F2
58	Mean	5.7	3.9	-0.1	-10.4
n=17	S.D.	0.6	0.5	6.8	7.2
61	Mean	8.1	3.5	-2.7	-9.8
n=17	S.D.	1.5	0.7	3.8	3.7
Total	Mean	6.9	3.7	-1.4	-10.1
n=34	S.D.	1.6	0.6	5.6	5.6

Table 5.3 Distance and visual angles during head fixations for Pattern 2 subjects.

5.8.2 Standard Depth Task (SDT)

The eye-key distance and viewing angles for both subjects filmed while performing the SDT can be found in Table 5.4. In contrast to the Pattern 2 discrimination, these birds were found to have an extra head fixation (F2A) occurring at a mean eye-key distance of 4.6cm.

At F1, subjects were again aligned midway between the two response keys. From F1, the subject repositioned in front of one of the two keys at F2A. If the key chosen was correct, the subject would emit a peck thus completing the trial. When the choice was incorrect, the subject would re-align with the opposite key (but now at F2) before emitting the final peck. The probability of F2A occurring was equal to that of F2. As in the Pattern 2 discrimination, F2 was always present for the SDT. However, this rule breaks down during

threshold testing (see Section 5.8.3). The difference between the mean F1 and F2 eye-key distance was equal to that seen in the Pattern 2 group (3.2cm).

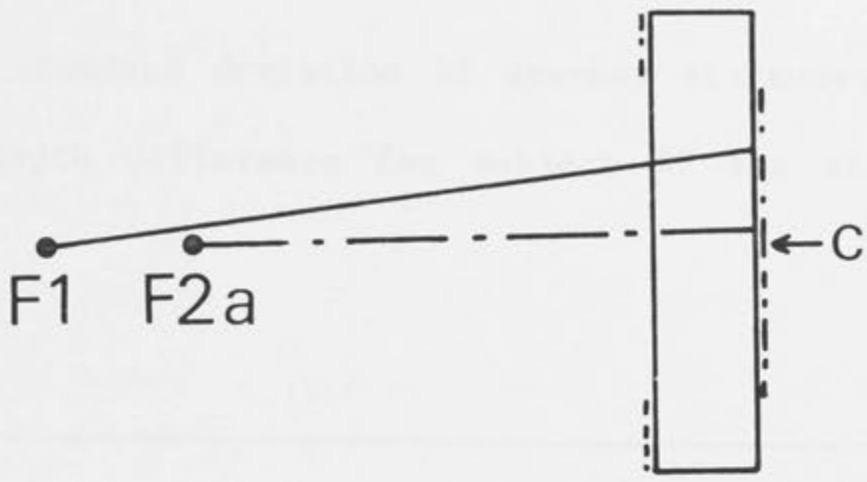
Subject		Eye-key distance (cm)			Viewing Angle (α°)		
		F1	F2A	F2	F1	F2A	F2
56	Mean	6.0	4.4	2.9	-7.4	-1.1	2.1
n=17	S.D.	0.5	0.3	0.8	4.0	5.5	10.8
47	Mean	6.0	5.3	2.7	-14.3	-9.2	-9.5
n=17	S.D.	0.4	0.4	0.4	6.7	4.2	7.8
Total	Mean	6.0	4.6	2.8	-10.9	-3.2	-6.4
	S.D.	0.5	0.5	0.5	6.4	6.4	10.0

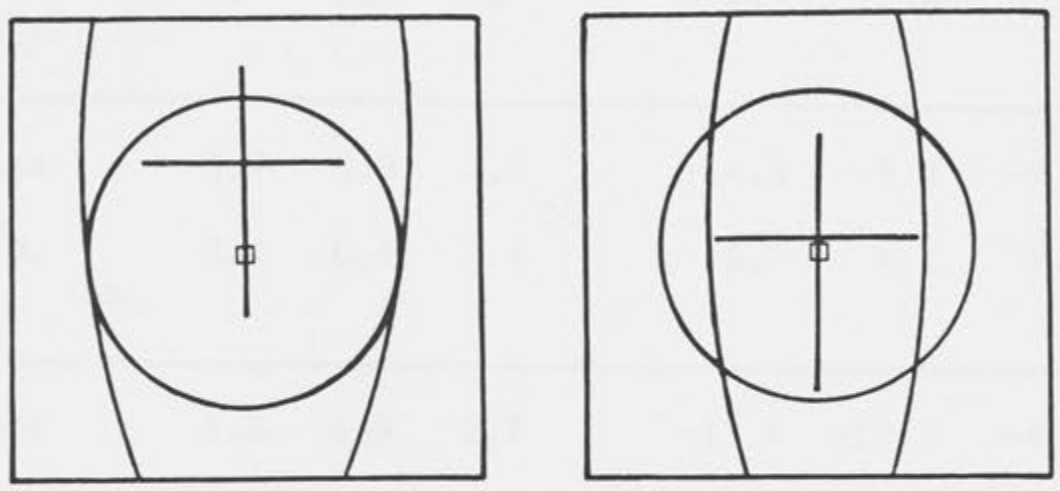
Table 5.4 Distance and visual angles during head fixations for SDT subjects.

The head fixations allow time to process visual information, and the data strongly implicate F2A as the point at which the most critical decision to peck was made. From the mean viewing angle found for F2A, it was possible to project the position of the binocular field onto the stimulus. The resulting picture shown in Figure 5.8A was drawn assuming for simplicity that the subject was aligned with the tip of the beak directed towards the centre of the horizontal axis of the key.

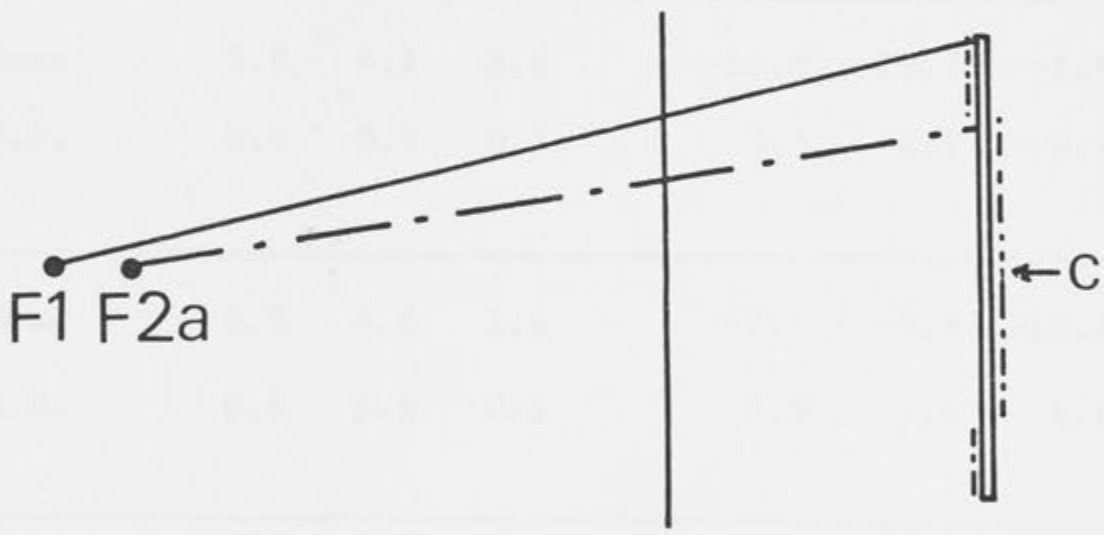
Figure 5.8 Projection of the binocular field onto the positive stimulus in the Standard Depth Task (SDT) (A) and during threshold testing on the SDT (B). The centre of the stimulus (C) is marked by the small square in the frontal views. The centre of the binocular field is indicated by the large cross, and the curved lines show the field borders. The solid and interrupted lines from the F1 and F2a fixations show the mean eye-beak axis.

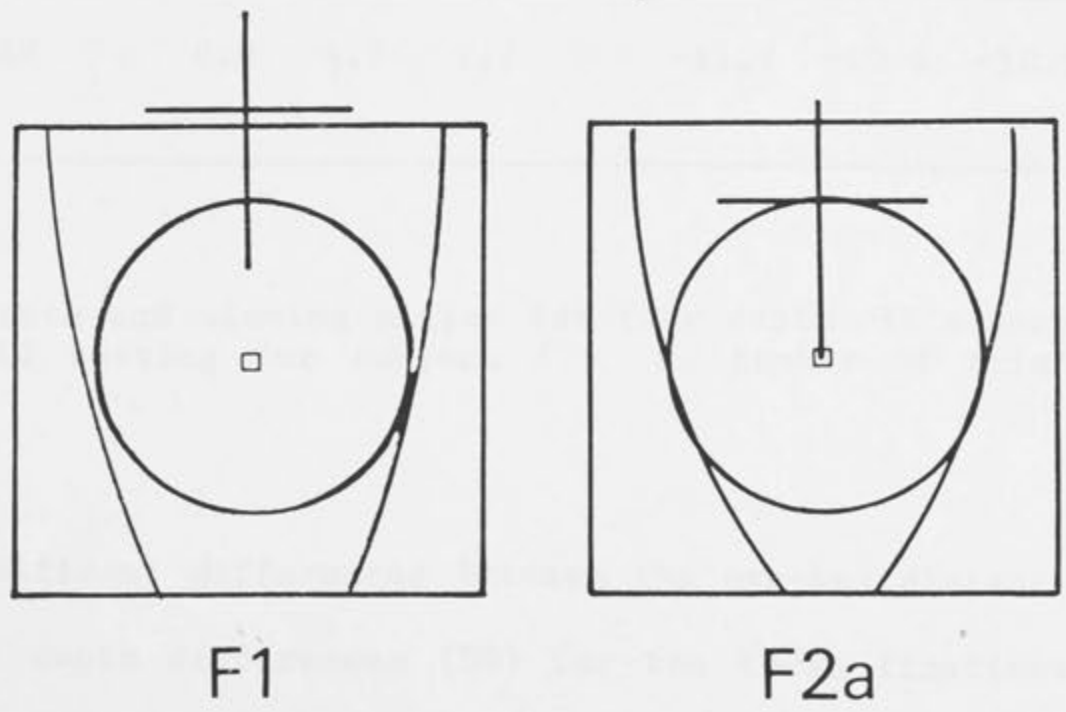
A.





B.





5.8.3 SDT Thresholds

The mean and standard deviation of eye-key distances and viewing angles for each depth difference for subject 47 are shown in Table 5.5.

DD(mm)	n		Eye-key distance (cm) F1	F2A	F2	Viewing Angle (α °) F1	F2A	F2
10	17	Mean	6.0	5.3	2.7	-14.3	-9.2	-9.5
		S.D.	0.4	0.4	0.4	6.7	4.2	7.8
6	15	Mean	5.8	4.9	2.7	-13.4	-13.2	-9.1
		S.D.	0.6	0.8	0.4	3.5	2.9	8.1
3	17	Mean	5.8	4.1	2.6	-11.8	-13.3	-8.8
		S.D.	0.4	0.5	0.3	3.5	4.7	6.4
1	9	Mean	6.5	4.6	2.6	-7.1	-6.6	-13.4
		S.D.	0.6	0.5	0.5	7.5	5.6	4.1
		MEAN	6.0	4.7	2.7	-11.7	-10.6	-10.2

Table 5.5 Distance and viewing angles for four depth differences (DD) during threshold testing for subject 47; n, number of trials analysed.

There were no significant differences between the eye-key distances at each of the four depth differences (DD) for the three fixations.

These correspond with F1, F2A and F2 described for the SDT. It is interesting to note that as the depth difference was decreased thus making the discrimination more difficult, the frequency of the F2A fixation increased while F1 became less frequent. F2A occurred on 88% of the trials for a 3mm depth difference, and always occurred during the 1mm depth difference discrimination. For the latter depth difference, F1 occurred on only 40% of the trials.

It can be seen from Table 5.5 that the mean viewing angle of the stimulus at F2A was 11° below the eye-beak axis rather than coincident as seen for the SDT group. When the projection of the binocular field was examined in relation to the positive stimulus, it was found that the subject had effectively centered the binocular field on the disparity break at the edge of the displaced circle (Figure 5.8B).

5.8.4 LACE Task

5.8.4.1 *Binocular (Group 3A)*

The results for the LACE group were similar to that seen for the SDT group. The eye to key distances and viewing angles are detailed for each subject in Table 5.6.

Again these subjects showed more head fixations during the peck sequence than the Pattern 2 group, with the mean number of fixations for all subjects equal to 2.6. All birds adopted the same stereotyped behaviour patterns seen for the birds filmed while performing the SDT, except subject 57. This subject always aligned with the left key at F2A, without recourse to an initial F1 fixation.

Subject		Eye-key distance (cm)			Viewing Angle (α °)		
		F1	F2A	F2	F1	F2A	F2
59	Mean	4.5	3.8	2.0	-9.5	7.2	14.7
n=21	S.D.	0.7	0.7	0.6	8.4	6.3	9.5
55	Mean	5.7	4.1	2.4	-7.2	3.1	11.3
n=15	S.D.	0.5	0.5	0.5	3.5	3.4	6.0
57	Mean	-	4.6	2.3	-	-19.9	-8.6
n=20	S.D.	-	13.0	0.4	-	7.4	12.8
68	Mean	5.7	3.7	2.2	5.6	5.0	9.0
n=17	S.D.	0.7	0.4	0.4	6.9	5.2	5.2
67	Mean	8.2	5.6	3.7	-16.8	1.8	12.6
n=19	S.D.	0.7	1.0	0.3	7.1	5.4	3.2
48	Mean	7.0	4.4	2.6	15.8	17.6	27.3
n=14	S.D.	1.1	1.1	0.9	4.4	5.0	4.5
	MEAN	6.2	4.4	2.5	-2.4	2.5	11.1

Table 5.6 Distance and viewing angle during head fixations for subjects trained on the LACE task.

In moving from F1 to F2A to F2, most subjects adopted an alignment change which resulted in the centre of the stimuli being positioned from slightly below the eye-beak axis to slightly above. All subjects showed this shift in α, as if the fixations occurred on a continuous pecking arc. The mean viewing angle for all subjects was again near the AP zero plane, although the standard deviation indicates that there was a considerable range in individual viewing angles.

5.8.4.2 *Monocular (Group 3B)*

Performance under monocular conditions was clearly different to the stereotyped binocular behaviour. Both subjects adopted a system of false pecking in which the peck was too soft to depress the key. False pecks were more frequent for subject 67 who often directed the peck around the response key rather than at the key. During a false peck subject 67 often stopped mid-peck with the beak opened and the eyes half closed. After a brief fixation the head was withdrawn. A mean of 3.0 false pecks occurred per trial for subject 67. The frequency increased if the correct key was positioned on the blind side of the bird.

For subject 68, false pecks occasionally occurred. An additional tactic was to initiate a final peck stopping mid-peck with the tip of the beak half open and resting on the response key. During this fixation, unlike subject 67, the eyes were always fully open. This subject also engaged in much more movement without the movement constituting a peck. The movement was always and only directed towards the key. The total number of fixations varied from 2 to 21 with a mean of 3.8/trial. The eye-key distance during a fixation was always less than 4.5cm indicating that the F1 fixation seen in normal binocular birds was entirely absent. Nor did the fixation distance

appear in any temporal order. The mean distance for 111 trials was 3.4cm (σ_{n-1} = 0.9 cm) (see Table 5.7).

Monocular fixations sometimes occurred immediately prior to a peck or false peck. The bird always realigned binocularly before emitting the peck. In general however, both birds observed the keys directly at a viewing angle that was always well within the "binocular field" (Table 5.7). The mean angle over 111 trials was equal to +3.4° (σ_{n-1} = 7.6°).

Subject		Eye-key distance (cm)		Viewing Angle (α °)	
		A	B	A	B
68	Mean	3.6	3.0	2.3	4.9
n=61	S.D.	1.1	0.8	7.4	7.0
67	Mean	3.2	3.6	2.0	4.4
n=50	S.D.	0.8	0.7	8.0	8.0
	MEAN	3.4	3.3	2.2	4.7

Table 5.7 Distance and viewing angles during head fixations for monocular subjects performing the LACE task: A, correct key on visible side ; B, correct key on blinded side.

5.9 DISCUSSION

5.9.1 The Relative Position of Head Fixations

The results of the video analysis of head fixations during discrimination performance can be grouped into three distinct classes based on the type of behavioural test. These are pattern, binocular depth and monocular depth. During the pattern discrimination there occur only two head fixations as reported by Goodale (1983a). The absolute eye-key distances are less than those reported by other authors (Hodos *et al.*, 1976; Goodale, 1983a). However, the size of the stimulus was considerably larger (4.5cm sq.) than the standard 2.5cm keys used by the above authors. The mean fixation distances for all tasks are shown in Table 5.8. It can be seen that except for subject 61, all F1 distances were remarkably similar. So too were the distances between the first and last fixations (F1-F2).

Task	F1	F2A	F2	F1-F2
Patt 2	6.9	-	3.7	3.2
SDT	6.0	4.6	2.8	3.2
SDT-Thresh.	6.0	4.7	2.7	3.3
LACE	6.2	4.4	2.5	3.7

Table 5.8 Mean eye-key distances for each head fixation seen for four discrimination conditions. Distances are in cm.

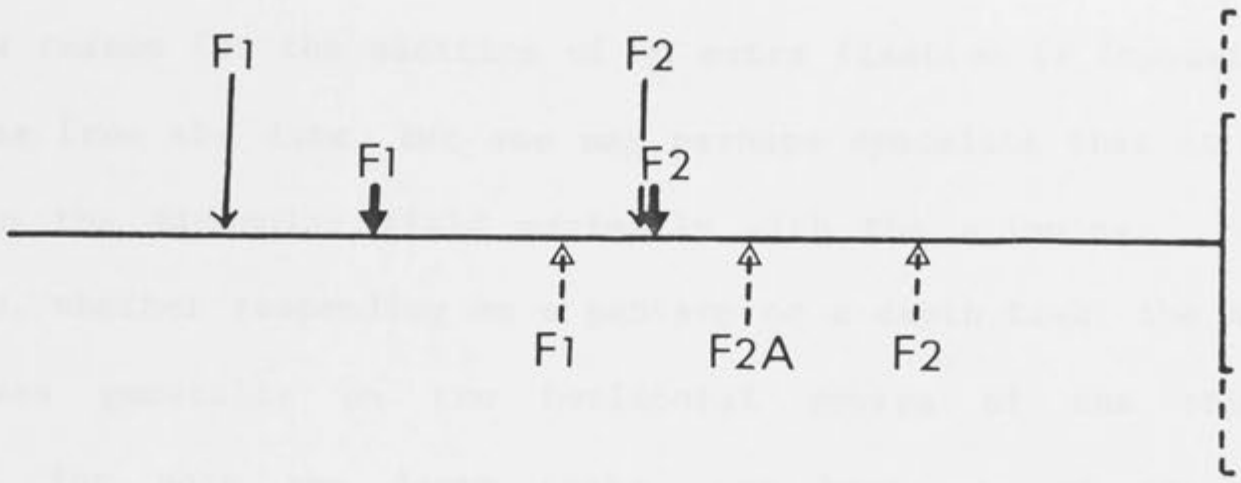


Figure 5.9 Position of head fixations found in this study (⇧) compared with those found by Goodale (1983) during a pattern location task (⬇) and during pecking at grain (↓).

The mean F-stops for all four discrimination conditions of Table 5.8 are presented in Figure 5.9. Shown for comparison are the F stops found by Goodale (1983) for both free feeding and a feature positive pattern discrimination. It can be seen that there appears to be little correlation between the absolute positions of the fixations for the different studies, particularly F1.

5.9.2 Head Fixation and Binocular Field Position during Binocular Depth Discrimination

In contrast to the behaviour of birds filmed during a pattern discrimination, all subjects trained on a depth discrimination made an additional fixation stop. This extra fixation (F2A) was interposed between F1 and F2. Since the probability of F2A occurring was equal to that of F2 occurring, and since for both F2A and F2 the subject was positioned directly in front of one of the keys, it would appear that F1 served to align the subject with one of the two keys, while the main decision to peck was made at F2A. As the SDT became more difficult during threshold testing, the frequency of the F2A fixation increased, while the frequency of F1 occurring decreased. However, the absolute distances for all three fixations did not vary when the depth difference was decreased.

The reason for the addition of an extra fixation is impossible to determine from the data, but one may perhaps speculate that it served to align the binocular field maximally with the stimulus. For all subjects, whether responding on a pattern or a depth task, the AP zero plane was generally on the horizontal centre of the stimului. However, for both the depth tasks, the best use of the narrow binocular field for enhancing the binocular depth cues present in the positive stimulus, was to direct the binocular field at one or other of the stimuli. Indeed, this is what appeared to occur during F2A. Thus aligned, the projection of the binocular field encompassed the upper and lower borders of the displaced circle in the D10 stimulus (Figure 5.8A), and covered the entire edges of the circle during threshold testing (Figure 5.8B). In this latter case, the centre of the binocular field was aligned more with the edge of the circle where the disparity breaks occurred.

From the above data, it would appear that the decision to peck one of the keys occurred at F2A. At F2, subjects always closed their eyes and opened the beak such that the eye was fully closed by the time contact occurred. The ballistic nature of this response, combined with the fact that subjects were never observed to 'change their minds' at this point makes it unlikely that the discrimination choice was made at F2. Once begun, the peck was carried to completion, so ending the trial.

In determining the threshold acuity in Chapter 3, the distance from the pupil to the front surface of the key was taken at both F1 = 6.0cm and F2A = 4.7cm, thus covering the range in which the decision to peck was presumably made. However, the latter value is likely to give the most accurate acuity threshold.

5.9.3 Analysis of Monocular Cues in the LACE Task

Given the viewing distance of the pigeon, it is also possible to analyse how the depth stimulus (LACE 6) appears when viewed without binocular depth cues. The LACE Task was primarily developed to produce a stimulus in which retinal disparity was present over the entire stimulus. This maximised the area of the stimulus in which binocular depth cues were present. The density of the array was reduced to lessen the salience of both motion parallax and overlap of individual elements during oblique viewing, as possible monocular cues to depth. From Figure 5.10, it can be seen that the minimum viewing angle in the horizontal plane for which the first sign of overlap occurs is 34°. Hence no overlap will occur when viewing from position I, corresponding to the F1 fixation, or when viewing stimulus A at position II, corresponding to the F2A fixation. However, from position II, viewing of stimulus B can also occur with the left eye, and strong overlap of elements may be present on the far left of the stimulus. However, behavioural tests described in Section 4.3.2.1 indicated that this small amount of overlap was not sufficient to be an operative cue.

Stronger candidates for confounding monocular cues are motion parallax and accommodation. It was observed that the two subjects who performed reasonably well on the LACE Task (after much training) appeared to use movement, often in the form of a false peck. The direction of movement was always in the posterior-anterior direction, and could serve to rapidly change the relative focus of the two planes present in the positive depth stimulus. Such movement would not, however, be effective for utilization of motion parallax as a cue to depth. Here, movement would best be in the medial-lateral direction rather than the posterior anterior-direction seen in practice.

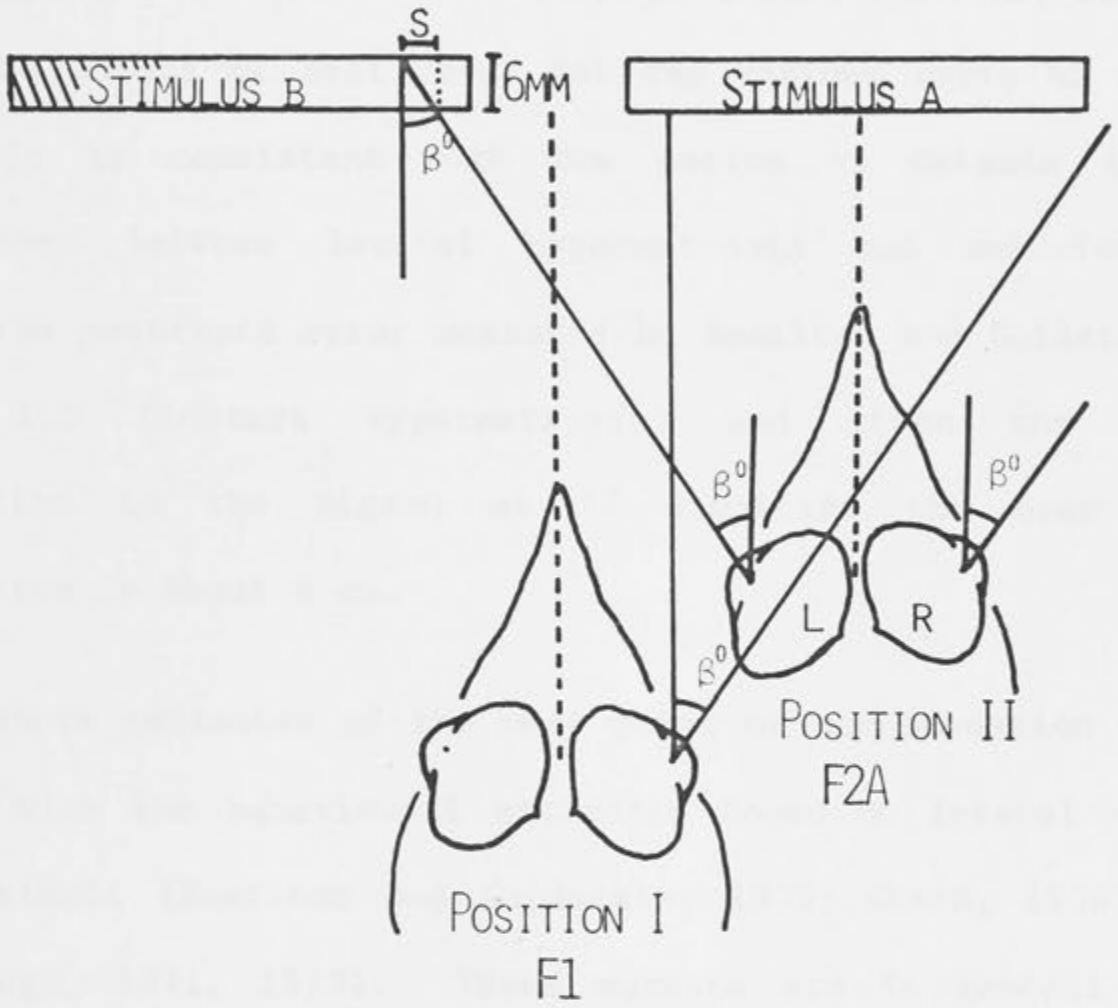


Figure 5.10 Geometrical determination of possible overlap of individual triangles as a monocular cue to depth in the LACE 6 stimulus. The minimum angle of overlap (β °) was calculated from the minimum distance between elements (s = 4mm). Thus it can be seen that overlap only occurs on the far left side of stimulus B when viewing from position II with the left (L) eye. No overlap is present when viewing from position I.

The range of accommodation of the pigeon eye has been reported to be about 17 Dioptres (Gundlach *et al.*, 1945). Nye (1973) calculated from ray tracing diagrams obtained from frozen sections through the pigeon eye, that the least distance at which objects first appear in focus (near point of accommodation) was about 4.5cm in the lateral field and about 3cm in the anterior binocular field. Since the accommodative state was undetermined, these values cannot be considered as absolute. However they do demonstrate the relationship between the points of best focus for the various parts of the visual field. It is consistent with the notion of Catania (1964) who distinguishes between lateral hypermetropia and anterior myopia. Based on the ametropic error measured by Hamilton and Goldstein (1933) (0.5 - 1.5 Diopters hypermetropic) and given the range of accommodation in the pigeon as 17 dioptres, the near point of accommodation is about 6 cm.

The above estimates of the near point of accommodation are not in agreement with the behavioural estimates based on lateral viewing of distant stimuli (Hamilton and Goldstein, 1933; Chard, 1938; Catania, 1964; Blough, 1971, 1973). These authors are in general agreement that the near point of 'accommodation' in the lateral fields, as measured behaviourally, is about 40cm. The large range of accommodation of the pigeon eye may reflect that accommodation serves both the central fovea for viewing distant objects in the lateral field and the specialized temporal retina subserving the frontal binocular field.

In the present study, it was found that the number of head fixations increased during monocular viewing but lost the well-defined temporal position order evident in normal binocular birds. Instead subjects tended to remain within a limited 3-4cm range of the key and

rarely viewed the stimulus with full monocular regard. Moving towards the stimulus within this range could thus produce an accommodative based monocular cue in which one of the planes of the depth stimulus would appear out of focus. This would also account for why subjects needed to observe the key so closely with the eyes opened, unlike that seen in the normal peck reponse.

5.9.4 Summary

In summary, the photographic analysis of the behavioural peck response during discrimination performance indicates that an extra fixation (F2A) occurs in the depth tasks that is not seen in the pattern task. One of the effects of the F2A stop is that the binocular field is fully aligned with the stimulus, thus maximising the chances of detecting depth by a binocular cue. This provides further support for the results of Chapter 2. Here it was shown that the depth task was difficult to discriminate on the basis of monocular vision alone. However, monocular performance did improve given enough training. Similar results were seen on a related task (LACE Task) reported in Chapter 4. Analysis of monocular performance on this task reveals that accommodation, not motion parallax, appears to be a possible effective monocular cue.

The large differences in behaviour between monocular and binocular discrimination further emphasize that the cues used under the two situations are radically different.

CHAPTER SIX

GENERAL DISCUSSION

CONTENTS PAGE NO.

6.1 GENERAL DISCUSSION

6.1.1 The Main Findings of This Thesis

The results of this thesis support the hypothesis that the pigeon can perceive depth through the utilization of binocular vision. The behavioural evidence in support of this hypothesis is that pigeons are capable of discriminating depth in variations of the 'Frisby' stimulus. These targets contained both convergence and retinal disparity as cues to depth. It was shown tht performance on the depth discriminations was superior under binocular rather than monocular conditions. The binocular superiority was evident whether monocularity was induced by covering one eye or by surgically disconnecting the two half brains. Analysis of performance after progressive commissurotomy revealed that integration between components of the tectofugal pathway were necessary for the binocular discrimination of depth. In contrast, the telencephalic target of the thalamofugal pathway (the visual Wulst) could be bilaterally lesioned without affecting the depth discriminations, even when performance was measured at the best psychophysical limits of depth perception. The binocular acuity of the pigeon was found to be 1 minute of arc for a luminance of 2.7 log cd/m^2. This binocular acuity is better than the spatial frequency acuity measured by other authors (Nye, 1968; Blough, 1973; Hodos *et al.*, 1976; Hodos and Leibowitz, 1977) and surpasses the sampling mosaic of the retina. Thus, the pigeons' binocular depth acuity is in the realms of hyperacuity and is likely to reflect functional stereoacuity. It was also found that the pigeon has an ovoid shaped binocular field maximal and symmetric about the eye-beak axis.

6.1.2 The Dual Visual System

The pigeon has been described as having a dual visual system including a central fovea serving the lateral visual fields and a second specialized region which mainly receives input from the binocular frontal field. This latter region in the temporal retina, referred to often as the 'red-area' because of the concentrtion of red oil droplets, lacks a fovea but is characterized by increased ganglion cell density and synaptic complexity (Yazulla, 1974).

The separate projections of the two specialized regions of the retina describe the 'visual trident' (Rochon-Duvigneaud, 1933, see Walls, 1942). Such a subdivision has thus been ascribed as the functional basis for two separate modes of survival:

> "The pigeon must be near-sighted if it is to see, directly in front of its beak, the food that it eats, whereas it must be farsighted if it is to see, in the lateral 'panoramic' field, the approach of predators from a distance." (Catania, 1964)

Polyak (1957, see Catania, 1964) commented that just prior to pecking, the eyes are used 'simultaneously in a binocular stereoscopic way'. Recent evidence has shown that coordinated vergence eye movements occur in response to a stimulus presented within the binocular field (Bloch *et al.*, 1981; Martinoya *et al.*, 1982). Such a pattern has not been observed in the lateral fields. Thus, the pigeon has a field of vision in which binocular overlap occurs, and eye movements act in an integrated fashion within this field. Taken together with the results of this thesis, there is little doubt that the pigeon can perceive near objects binocularly in depth.

6.1.3 The Functional Use of A Binocular Depth Mechanism

As a granivorous bird, the functional use of a binocular depth mechanism in the pigeon would most likely be for pecking at grain. A stereoacuity of 1 minute of arc would allow the detection of a depth difference, at a pecking distance of 55 mm (see Goodale, 1983) and an internodal distance of 24 mm, of 0.1 mm.

The peck response of the pigeon is ballistic in the final stages (Hodos *et al.*, 1976). In order to successfully pick up a desired object (e.g. a piece of grain), the bird must be able to locate it accurately with a margin of error much less than the absolute height of the grain. It has been shown that the gape size varies as a function of the location and size of the target (Zeigler *et al.*, 1980). Thus the observed acuity will also allow the accurate determination of how much the mandibles should be opened at the point of beak-grain contact.

It is theoretically possible that a binocular depth mechanism is also used to locate objects at much greater distances than within the pecking range. In the present thesis depth perception was only examined for near viewing distances. However, frontal acuity decreases the greater the distance of an object in the binocular field (Bloch and Martinoya, 1982), the best visual acuity occurring for objects within pecking range (less than 10 cm). Thus, it is more probable that motion parallax would be the critical factor in spatial depth analysis for viewing objects in depth at great distances (such as while flying). Further research is needed to enucleate the critical features involved in spatial localization of distant objects in the pigeon.

6.1.4 The Location of the Binocular Field

Given that the binocular quality of the frontal field of the pigeon is used for pecking at grain, the most efficient position of the binocular field would be to centre the field on the object of regard at the time at which estimation of the depth of the object occurs. Furthermore, it would be expected that at this point in time, the piece of grain would be imaged on the temporal area dorsalis for maximal use of the retinal specialisation.

It was shown in Chapter 5 of this thesis that the maximum width of the binocular field occurred about the eye-beak axis. Hence any object of regard should also be positioned in this plane. Indeed Goodale (1983a) has shown that pigeons pecking at grain approximately align the eye-beak axis with the grain prior to the final ballistic portion of the peck response (at F2).

It was also shown in this thesis that the maximal width of the binocular field was 24° for conditions in which each eye had diverged about 3° from the primary eye position. Thus, to view a piece of grain at a distance of 55 mm, each eye would have to converge and the width of the binocular field would increase. With the aid of the schematic eye of the pigeon described by Marshall *et al.* (1973) and the isodensity map of the ganglion cell distribution detailed by Binggeli and Paule (1969), and the aid of a cross section of the pigeon eye (see Gundlach *et al.*, 1944) it can be calculated that the angle between the edge of the retina and the centre of the increased ganglion cell specialisation in the red field (area dorsalis) is 18.3°, and the angle between the area dorsalis and the central fovea is 57°. Hence, in order to image an object on both 'area dorsalis' each eye would have to converge and the binocular field width at a viewing distance of 55 mm would be approximately 33°.

6.1.5 The Neural Localisation of a Binocular Depth Mechanism

Cells sensitive to binocular disparity have been found in the superficial laminae of the visual Wulst of the owl (Pettigrew & Konishi, 1976a) and the kestral (Pettigrew, 1979), both predatory birds. No such substrate for stereopsis has yet been found in the pigeon Wulst (Frost *et al.*, 1983). However, it is technically difficult to simulate perfect convergence on a nearby point in a lateral eyed bird under conditions of anaesthesia.

In the present thesis it was shown that the visual Wulst of the pigeon was not required to discriminate a depth difference of 1 minute of arc. The remainder of the visual system was capable of mediating the depth discrimination. The dorsal supraoptic decussation is known to be a bilateral link in the thalamic hyperstriatal pathway. Again, normal behavioural performance was found after transection of this commissure. It is possible that behavioural deficits in binocular depth perception do occur after such lesions, but were too subtle to be detected by the behavioural tests used. It would be of interest to examine the role of the Wulst in the discrimination of dynamic random dot stereograms. This also raises the question of whether the pigeon can solve local disparity ambiguity and has the capacity for global stereopsis.

In contrast to the puzzling role of the thalamofugal pathway in binocular depth perception in the pigeon, the commissures at the level of the tectum (both the posterior and tectal commissures) do participate in the binocular integration of monocular visual information. It is possible that they are involved in the pre-requisite convergence eye movements needed for binocular single vision rather than directly integrating signals of a local stereoscopic mechanism. Further research needs to be done to clarify this point.

The results of these lesion studies perhaps demonstrate the interrelationship between motor output and sensory input. Schneider (1969) distinguished between the role of the superior colliculus and the role of visual neocortex in mammalian vision. His 'two visual systems' hypothesis ascribed the function of 'orientation' behaviour (enabling an animal to localise a stimulus in visual space) to the phylogenetically older pathway from retina to superior colliculus, whereas the more recently evolved geniculostriate system participates in the 'identification' of that stimulus. The thalamofugal system in the pigeon may access appropriate motor pathways in part by modulating the input/output functions of other retinofugal systems.

6.1.6 The Evolution of Binocular Vision

Although it is known that both the toad (Collett, 1977) and the praying mantid (Rossel, 1983) utilize convergence as a cue to absolute distance, there is no evidence that these animals use retinal disparity as a cue to depth. The existence of stereopsis has only been demonstrated in man, some primates and mammals and in birds of prey, either by the existence of local disparity detectors or by the ability to solve global stereoscopic problems. Thus, this thesis presents the first demonstration of the use of retinal disparity as a cue to depth in a bird which does not hunt and catch prey and retains the advantages of panoramic vision with laterally placed eyes. The existence of stereopsis in the pigeon implies that stereopsis is not limited to an elite class of animal which has a predatory lifestyle. Rather, stereopsis may be present in all vertebrates which have the capacity for binocular vision. In addition, the findings of this thesis emphasize that the frontal placement of the eyes is not a prerequisite for stereopsis, but serves only to increase the static operational range of binocular vision.

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